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# THE NEUROFIBRIL HYPOTHESIS

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NERVE cells and reproductive cells share honors in being the most complex cytological elements in the bodies of the higher animals. The cellular nature of the egg and of the spermatozoon was early recognized by the pioneer workers in the field of animal cytology, but it required over half a century of investigation to make clear the true character of the nervous elements. The Cell Theory, proposed by Schleiden and Schwann in 1838–39, was not successfully applied to nervous tissues till 1891. Before that time nerve fibers, ganglion cells, fibrillar material, sense cells and the like afforded a confused mass of elements which were assumed to serve as a basis for nervous organization.

Nerve fibers were apparently first described by Fontana in 1781 (Fig. 1), two years before Monro (1783), in his *Observations on the Structure and Functions of the Nervous System*, called attention to them. They excited the interest of the early workers and were described in much detail by such masters in the use of the microscope as Treviranus (1816) and Ehrenberg (1833, 1836). Ganglion cells were first identified and described in 1833 by Ehrenberg, who published a more elaborate account of these bodies in 1836 (Fig. 2), the year in which Valentin (1836) described numerous nervous organs with their contained ganglion cells.

Five years after the discovery of these cells, that is in 1838, Remak, on the basis of his studies on the sympathetic system, declared that nerve fibers could be traced directly from ganglion cells. This conclusion was supported by Helmholtz (1842) and by Hannover (1843) in their descriptions of the nervous elements of invertebrates. In the work of all these investigators, however, it was not absolutely certain that the fibers found by them in connection with the ganglion cells were really nerve fibers. This uncertainty was removed by the discovery of Koelliker (1844) that in the vertebrates certain medullated fibers, about whose nervous nature there was not the least doubt, could be shown to be in direct continuity with ganglion cells. Thus the connection of ganglion cells and nerve fibers became an established fact.

## THE NEURONE THEORY

In 1855 Leydig pointed out in his study of the central nervous organs in spiders that these organs contain, in addition to nerve fibers and ganglion cells, masses of





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finely fibrillar material to which he gave the general name of punctate substance. Material of this kind was subsequently recognized as a constant ingredient in the gray portions of the spinal cord and of the brain in the higher animals. The interrelations of the punctate substance and particularly of the nerve fibers and the ganglion cells occupied the attention of students in this field of investigation from the middle of the nineteenth century till 1891, when the whole subject was fully reviewed by Koelliker in his presidential

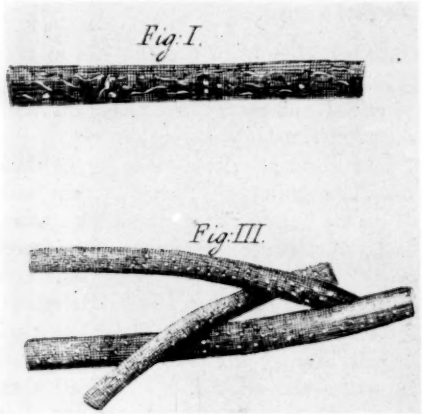


FIG. 1. FIRST ILLUSTRATIONS OF NERVE FIBERS
Fontana, 1781, p. 204, Tav. IV, Figs. I and III

address at the Munich meeting of the Anatomische Gesellschaft. This address, which was delivered in May, 1891, was followed in June of that year by Waldeyer's brilliant enunciation of the Neurone Theory, a theory that united in a truly remarkable way a vast array of facts brought to light by the earlier investigators.

According to this theory the nervous system is composed of numerous anatomically and genetically interrelated units or neurones each one of which consists ordinarily of three sets of parts: a nerve-cell body, one or more nerve-fiber processes, and numerous finely divided dendritic processes. Such a cell body with its processes constitutes a true nerve cell or neurone and this doctrine was found to be not only in agreement with what was known of the histology of the nervous elements but also with such embryological discoveries as those of His (1886), according to which nerve fibers were shown to be the outgrowths from the bodies of nerve cells. The year 1891 may therefore be looked upon as that in which the cellular interpretation of the nervous elements was first successfully accomplished, for the doctrine of the neurone has been to all intents and purposes universally accepted by the most competent students in the field of general neurology.

### THE NEUROFIBRILS

While the discoveries that led to the Neurone Theory were being made, the finer structure of the nervous elements was also being investigated. By such older workers in this field as Treviranus (1816), Ehrenberg (1833, 1836) and Valentin (1836), the contents of nerve fibers and of ganglion cells was believed to be a finely granular material of almost fluid consistency. In 1843 Remak called attention to the fact that in addition to this granular material the larger nerve fibers in the nerve cord of the crayfish possessed an axial bundle of some hundreds of very fine fibrils which ran in parallel courses along the length of the fiber. According to Remak these fibrils were best seen in the fresh condition of the fiber. Soon after a preparation of them had been made they disintegrated and the resulting granular material showed no trace of them. The year after these statements were put forth Remak (1844) published an excellent drawing of this condition in the crayfish (Fig. 3) and also described and figured a

ganglion cell (Fig. 4) in whose substance a system of fibrils concentric with the nucleus was clearly shown. No one can read Remak's descriptions or inspect his carefully drawn figures without being convinced that notwithstanding the very imperfect means at his disposal he saw with unusual clearness what subsequent investigators have been led to call neurofibrils.

### WHAT SCHULTZE THOUGHT

It was, however, Max Schultze above all others who raised these structures to a position of first importance. In several papers published in the decade beginning in 1863 this veteran histologist developed his views concerning the nature of neurofibrils. He believed that these bodies could be identified with certainty not

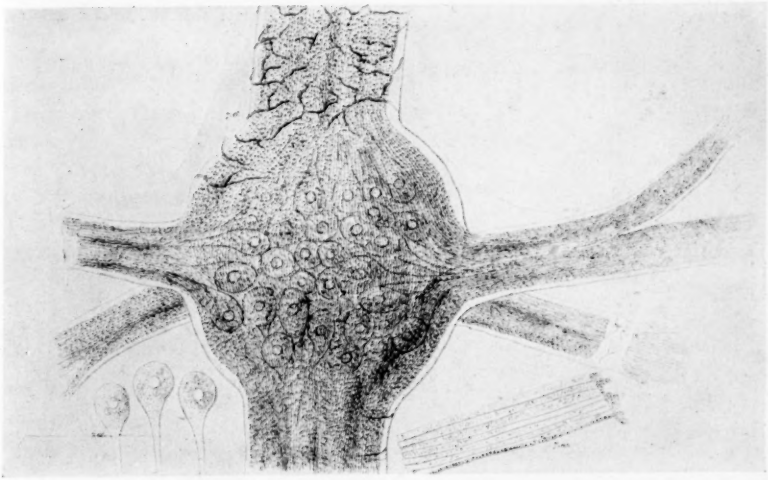

FIG. 2. FIRST ILLUSTRATIONS OF GANGLION CELLS FROM A GANGLION IN THE VENTRAL CHAIN OF THE LEECH

Ehrenberg, 1836, p. 721, Tab. VI, Fig. 7; *7.6*, the whole ganglion; *7.10*, connective nerve fibers; *7.12*, ganglion cells.

Remak's discovery of the neurofibril seems to have excited very little attention among the workers of his time, for in 1847 both Wagner and Bidder published on the structure of nerve fibers and of ganglion cells without intimating that these parts contained anything of a fibrillar nature. Nevertheless Leydig in his *Lehrbuch der Histologie* issued in 1857 referred to Remak's discoveries and described and figured fibrils as component parts of nervous tissue.

only in the axis cylinders of nerve fibers but also in the substance of ganglion cells (Fig. 5). Writing of the large cells in the brain of the Torpedo he stated (1871) that

> It was most convincingly shown here that the large cells removed from the living animal, and prepared in serum, in which they were capable of being easily isolated, possess both in their processes and in their proper substance, an exquisitely delicate fibrillar structure. . . . . Each of the numerous processes of these ganglion cells receives a compound fibril from the cell substance, giving the impression that the

whole mass of fibrils given off by ganglion cells only traverse it. The nucleus of these cells is seen with a sharply defined outline lying imbedded in the finely granular fibrillated material, but does not appear to stand in any direct connection with the fibrils which cover its external surface. . . . . We may regard such a ganglion cell, from which a peripherally directed nerve fiber proceeds, as representing the

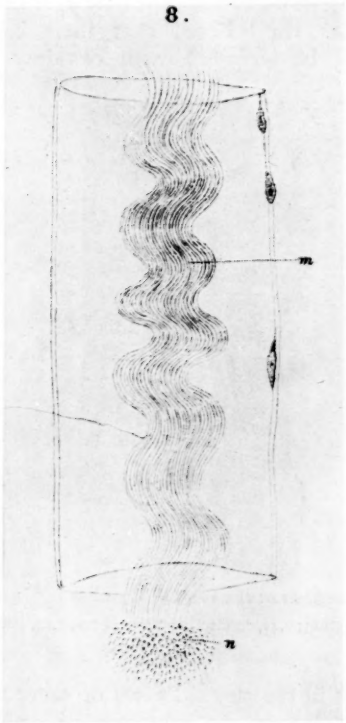


FIG. 3. FIRST ILLUSTRATION OF NEUROFIBRILS FROM A NERVE FIBER IN THE VENTRAL GANGLIONIC CHAIN OF THE CRAYFISH

Remak, 1844, p. 468, Taf. XII, Fig. 8

source and origin of this axis cylinder, but only in the sense that the fibrils which compose the axis cylinder are collected into a group from the arborescent processes of the cell; and thus the fibrils which are seen traversing the substance of the ganglion cell do not originate in the cell, but only undergo a kind of arrangement in it, and then pass to the axis-cylinder process, or extend into the other branched processes. . . . . The fibrils which emerge in a convergent direction from the cell substance, in order to form the axis cylinder process of the cells, unite, and are often far removed from one another by interfibrillar material. The formation of the proper axis cylinder results from a diminution of the interfibrillar material whilst the fibrils become more closely approximated in their parallel course, so that ultimately only a very small quantity of interfibrillar substance remains. . . . . I consider it, indeed, to be possible that, notwithstanding these observations, axis cylinders exist in which the original fibrillar nature is entirely lost by fusion of the fibrils with each other, and which have thus become homogeneous, but I regard the principle as correct, that the thicker axis cylinders

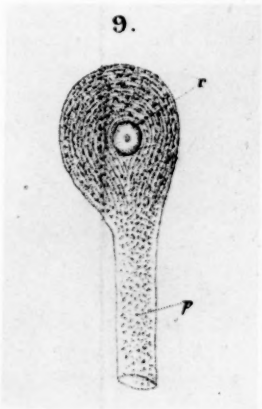


FIG. 4. FIRST ILLUSTRATION OF NEUROFIBRILS FROM A GANGLION CELL IN THE VENTRAL GANGLIONIC CHAIN OF THE CRAYFISH

Remak, 1844, p. 468, Taf. XII, Fig. 9

are composed of several primitive fibrils, since these converge at the centric, and for the most part separate from one another at the peripheric extremity. On physiological ground also I maintain the possibility of isolated conduction in these constituent fibrils, even when no trace of interfibrillar substance is present.

It is obvious from these extended quotations that Schultze believed not only in the presence of neurofibrils in ganglion cells and nerve fibers but also that these fibrils form the essential part of the nerve cell and are in fact the structures immediately concerned with that activity which is

the most fundamental of all nervous operations, namely, conduction. From this standpoint Schultze may be looked upon as the founder of the Neurofibril Hypothesis. During this period Frommann (1864 a, 1864 b) first stained neurofibrils using silver nitrate and thus added to the certainty with which they could be demonstrated; Deiters (1865) and Beale (1868) also described ganglion cells as bodies in whose substance fibrils could be identified.

Yet notwithstanding these fundamental discoveries and Schultze's clear statement of the Neurofibril Hypothesis these ideas attracted very little attention. Schultze's hypothesis was neither vigorously defended nor vigorously opposed. This apparent indifference was probably due to several circumstances. First of all the Franco-Prussian War, which extended from the summer of 1870 to the following spring, exercised a temporary retardation on all the intellectual activities of the times. Of more immediate importance perhaps than the war so far as the Neurofibril Hypothesis itself was concerned was Schultze's premature death in 1874. Possibly most of all was the absence of reliable methods by which neurofibrils could be clearly and unequivocally demonstrated. To the most expert of the early workers these delicate structures were at best only just within the range of visibility and their identification and investigation were consequently matters of extreme difficulty. Often sought for, they were seldom found and consequently an attitude of suspicion grew up about them that led many to deny their existence. This disbelief in the reality of neurofibrils was a common opinion at that time notwithstanding the fact that a reasonably satisfactory staining method for their demonstration had been devised by Frommann (1864 a) and later a much more satisfactory one by Kupffer (1883). But most of the new methods for the study of nervous tissues, as for instance the Golgi silver impregnation method (1875) and the methylen-blue technique (Ehrlich, 1886), were directed toward the grosser relations of fibers and cells rather than toward the finer structures within these parts. Consequently neurofibrils and their associated problems received relatively scant attention. Thus in the sixth

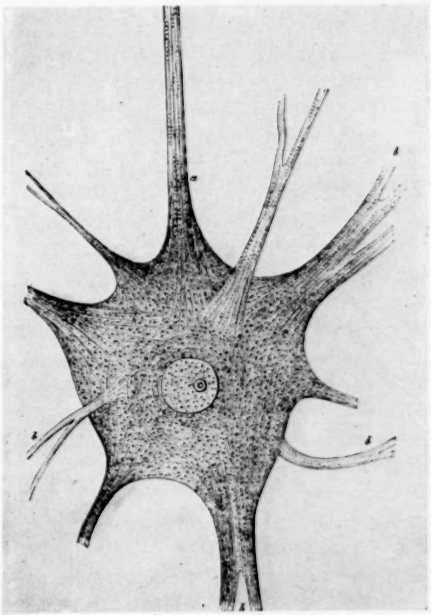

FIG. 5. GANGLION CELL SHOWING NEUROFIBRILS; FROM THE ELECTRIC LOBE IN THE BRAIN OF THE TORPEDO
*a*, neurite; *b*, dendrite. Schultze, 1871

edition of Koelliker's *Handbuch der Gewebelehre* published in 1896 neurofibrils are described as constituent parts of nerve fibers and of ganglion cells, but Koelliker's consideration of them contains nothing of importance that had not already been stated by Schultze in his general account in 1871. The period from the early seventies when Schultze made his mature declarations about neurofibrils till the

early nineties was a sterile one so far as neurofibrils were concerned. It was a period in which, as already pointed out, investigators worked on the relations of ganglion cells and nerve fibers rather than on the internal structure of these elements.

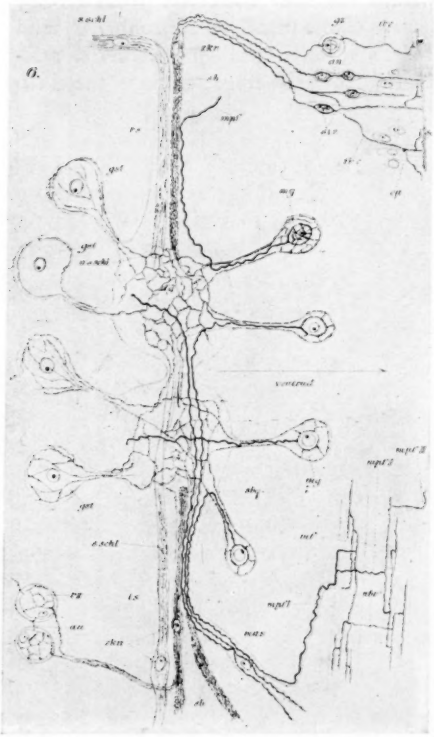

FIG. 6. DIAGRAM OF THE CONDUCTION PATHS ACCORDING TO APÁTHY IN A SOMITE OF THE LEECH

Apáthy, 1897, p. 748, Taf. 32, Fig. 6; *siz*, epithelial sense cells; *sb*, sensory bundle; *dg*, nerve-net in ganglion; *gst* and *mg*, ganglion cells; *mns*, motor bundles; *mf*, muscle fibers.

This period culminated in the nineties in what Bethe (1898 c, p. 96) appropriately called the "Golgi Enthusiasmus."

### THE WORK OF APÁTHY

But the Neurofibril Hypothesis even at this time was not without its earnest advocates. In 1889 Apáthy, a brilliant Hungarian histologist working for the most part at the Naples Zoölogical Station, issued a preliminary paper on the direction in which neurology should be reformed and in 1897 he published the first and what proved to be the only part of an extended monograph on the transmitting elements of the nervous system and their relation to the cells. In all of Apáthy's discussion the neurofibril is the fundamental structure. By several new methods of staining, particularly one based on the use of gold chloride, he succeeded in demonstrating neurofibrils with a clarity and distinctness such as had never been approached before. The drawings with which his extended monograph was illustrated showed neurofibrils with such remarkable clearness that many workers believed his figures to be over-enthusiastic attempts in the portrayal of histological details. His preparations, however, were exhibited at a great many scientific meetings at which histologists were present, and those who had the opportunity of examining them were forced to admit that his drawings were in no sense sharper than the details in his preparations. With the clearness of metallic wires neurofibrils could be traced in his preparations through tissue of unusual transparency. Unfortunately the methods by which these preparations had been made were extremely precarious. In the hands of most workers they yielded almost nothing and even Apáthy himself confessed that his own best efforts commonly resulted in complete failure. Nevertheless when the preparations were successful they exhibited neurofibrils as they had never been seen before.

### ARE NEUROFIBRILS CONTINUOUS OR NOT?

In such preparations, which were based in the main on material from the leech,

the earthworm, and like animals, neurofibrils could be traced according to Apáthy through sense cells, around whose nucleus they commonly formed a network, over nerves and into the central nervous organs (Fig. 6). Here they branched profusely, forming true networks, and as delicate fibrils they entered the bodies of unipolar ganglion cells to form a complicated fibrillar network extending through most of the peripheral protoplasm. From this network branches made their way inward toward the nucleus of the ganglion cell around which was formed a second or inner net, and from this inner net a coarse neurofibril emerged from the ganglion cell, and, after having passed through the central nervous organ again, made its way over a given nerve to a muscle which was thus innervated. In this way continuous neurofibrillar material was believd to extend from a sense cell on the surface of the animal through the central organ to a termination in a distant muscle. In the sensory portion of their courses the neurofibrils were described as fine, in the motor portion coarse. Thus the neurofibril rather than the cell was in Apáthy's opinion the all important element in the organization of the nervous system. Cells in fact were only roadways over which the neurofibrils travelled. These elements, though they started to grow within a given cell, soon spread, according to Apáthy, beyond it, penetrating the substance of other cells as they proceeded toward their final termination.

Apáthy's conception of nervous organization thus laid stress on a continuous neurofibrillar material and relegated nerve cells to a very subordinate position. In both these respects it was in radical opposition to the Neurone Theory. According to this theory nerve cells are the real units of nervous organization. In their early developmental stages as neuroblasts they had been shown to be distinct and separate bodies, whose subsequent union was established through the outgrowth of processes which eventually reached from cell to cell. It was the opinion of most neuronists that the processes from one cell never really fused with those from another but that they were at most simply in contact, a contact which in fact from time to time might even be broken and then reëstablished. Such points of contact, the so-called synapses, were definitely shown to be polarized, in that nerve impulses could pass over them in one direction but not in the other. Thus the advocates of the Neurone Theory emphasized a degree of discontinuity between the nerve cells that was in strong opposition to what Apáthy maintained.

As a result of these differences of opinion a lively debate arose on the question of neural continuity or discontinuity. While this discussion was in progress two new and important methods for the demonstration of nerve cells and neurofibrils were devised. These were Bielschowsky's ammonia-silver method first announced in 1902 and Ramón y Cajal's reduced silver method described one year later. Both methods were modified in a variety of ways and both were so successful as means of demonstrating neurofibrils that these bodies became the objects of active inquiry in many neurological laboratories. The problem that excited the interest of most workers was that already indicated, the degree of continuity or discontinuity between the nervous units. Among those who favored that amount of discontinuity implied in the Neurone Theory were Waldeyer (1891), Retzius (1905), Ramón y Cajal (1908a, 1908b, 1908c), von Lenhossék (1910) and others; the advocates of strict continuity included in addition to Apáthy (1897,

1907a), Bethe (1903), Bielschowsky (1908), Haller (1908), Wolff (1908), and Held (1905a, 1909). It must be admitted that the discussions that took place as a result of these differences of opinion led to no very definite conclusions. Many workers had the opportunity of examining at first hand the remarkable preparations made by Apáthy, but few were able to convince themselves that the preparations gave evidence of the kind of continuity claimed by him. Preparations that had been made in Bielschowsky's laboratory and that seemed entirely convincing to this worker failed to meet Ramón y Cajal's requirements of what a demonstration of continuity should be. Thus in general great uncertainty prevailed. (In a very recent paper Tiegs (1927) has revived the whole discussion by arguing against discontinuity.)

As a possible solution of some of these difficulties it was suggested that the nervous systems of different animals might be differently organized. In the higher forms where the synaptic system prevails discontinuity might be the rule. In the lower forms where the nerve-net is common continuity might obtain. Thus discontinuity might be expected in the nervous systems of one set of animals and continuity in those of another. Such an opinion was expressed by Sherrington (1906, p. 42) and was subsequently elaborated by Parker (1919). To what extent this view is sound is perhaps open to question, for Bozler (1927a) has recently given good reason for believing that the cellular elements in the nerve-net of the jelly fish *Rhizostoma* are quite as disconnected as is assumed for the synaptic system. Should this discovery by Bozler prove well founded, it may result in the complete overthrow of the idea of continuity, for if the synaptic nervous system is composed of discrete units and the same is shown to be true of nerve-nets, continuity as represented by continuous neurofibrillar substance between nerve cells would cease to be tenable. The synaptic system would differ then from the nerve-net only in that the former is polarized in the direction of its conduction and the latter not. In such a case neurofibrils in the nerve-net as well as in the synaptic system would be strictly intracellular structures.

### THE DEVELOPMENT OF NEUROFIBRILS

As a result of the introduction of the methods of Bielschowsky and of Ramón y Cajal great additions were made to what had already been known concerning neurofibrils. They were identified in the nerve cells of a wide range of animals from man (Laignel-Lavastine, 1906a) through all the groups of vertebrates (Tello, 1903, 1904; Michailow, 1908; Laignel-Lavastine, 1906b) to mollusks (Legendre, 1906a) and to worms (Ramón y Cajal, 1904; Kowalski, 1908, 1909; Ascoli, 1913; von Szüts, 1914b). Neurofibrillar nets were identified in receptor organs (Van de Velde, 1907), and in motor endplates (Boeke, 1926) and the pathology of neurofibrils was extensively investigated (Ramón y Cajal, 1906b; Marinesco, 1907; Gurewitsch, 1908; Schütz, 1909; Schaffer, 1909; Goodpasture, 1925). Perhaps most important of all was a series of contributions on the developmental history of neurofibrils (Held, 1905b; Brock, 1908, 1909; Fragnito, 1908; Gerini, 1908; Pesker, 1908; MacCurdy, 1909a, 1909b; Cowdry, 1914; Neal, 1915) from which three important conclusions may be drawn: first, neurofibrils develop at a stage much in advance of functional activity either sensory or motor; second, they begin their growth close to the nucleus of the neurone (Cowdry, 1914); and finally, they do not grow beyond the

limits of a neurone, that is, they are strictly intracellular (Gerini, 1908). Thus the application of new and improved methods added much to what had been known of these fibrillar bodies.

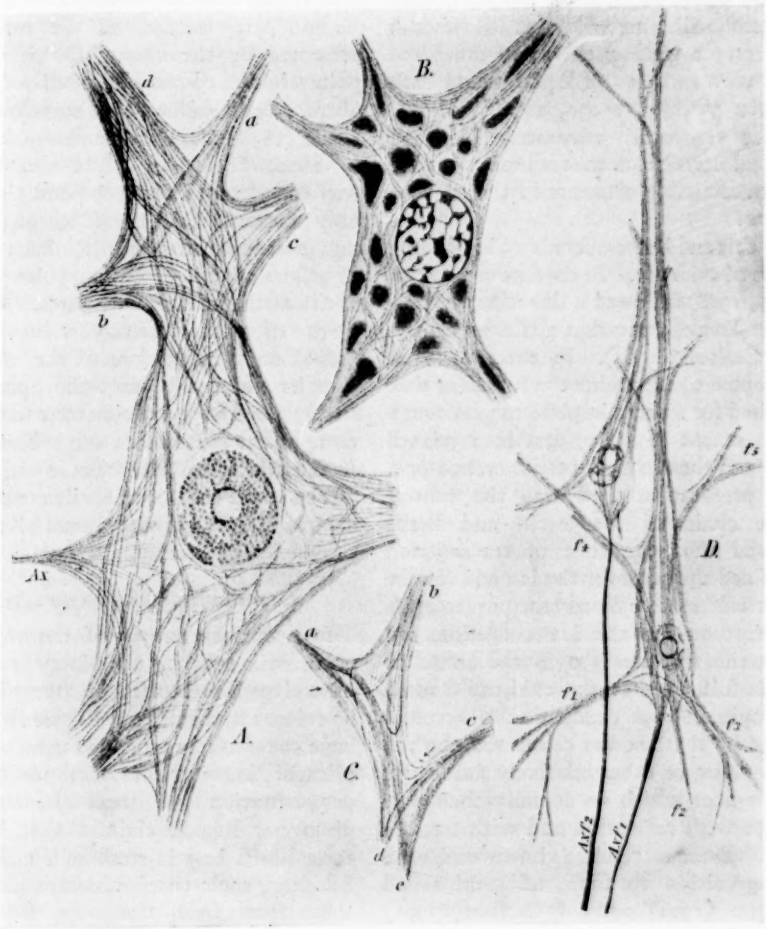


FIG. 7. GANGLION CELLS STAINED BY BETHE'S MOLYBDATE METHOD TO SHOW NEUROFIBRILS

Bethe, 1903, p. 59, Fig. 19; *A*, anterior-horn cell from man; *B*, cell from the nucleus of the facial nerve of the rabbit; *C*, dendrites from a human anterior-horn cell; *D*, human pyramidal cells.

### THE WORK OF BETHE

Most intimately associated with the modern investigation of neurofibrils is the work of Bethe, which beginning about three decades ago extended to within the last ten years or so. By novel methods, including the use of such delicate strains as toluidin blue, this indefatigable worker confirmed many of the details of Apáthy's investigations (Bethe, 1898a). According to Bethe (1900) neurofibrils maintain in general independent courses

over nerve fibers or through nerve cells, but in certain places true nerve-nets may be present (Fig. 7). In agreement with Apáthy Bethe declared for the continuity of neurofibrillar material, and his views in this respect were criticised in much the same way as those of Apáthy had been (Ramón y Cajal, 1903a, 1906b). Bethe further vigorously advocated Schultze's original declaration that neurofibrils were the transmitting elements in the nervous system.

To this end Bethe offered two interesting pieces of evidence. In the first of these he (1907, 1908) followed a line of experimentation devised somewhat earlier by Jenkins and Carlson (1904). In these tests he attempted to determine the length of time required for a nerve impulse to pass over a given extent of nerve, first in a relaxed state and then in a slightly stretched one. The preparation used was the ventral nerve chain of the leech, and Bethe claimed that the time of transmission remained the same for the lax and for the stretched state. Since the neurofibrils are tortuous in the lax condition and approximately straight in the stretched one it follows that the evidence favored the opinion that conduction is accomplished by these bodies rather than by the neuroplasm or other relatively fluid parts of the fiber which do actually change in length with relaxation and with stretching. Bethe's results, however, were in opposition to those of Jenkins and Carlson (1904) and of Carlson (1905) alone; in the work of these two investigators it was shown that the time of transmission did increase with stretching, a condition which indicated that the transmitting agent was fluid rather than solid. In consequence of this fact as well as of the further one that Bethe's observations were carried out on a piece of central nervous organ and not on a bundle of nerve fibers as those of Jenkins and Carlson were, Bethe's experimental test has not been accepted as crucial.

A second line of evidence introduced by Bethe (1910) turned on the condition presented by the neurofibrils at certain points in the course of medullated nerve fibers. Bethe believed in common with Mann (1898) that at the nodes of Ranvier in these fibers the fluid neuroplasm was completely interrupted and that the only elements that passed through this region were the neurofibrils. Such a state of affairs would of course point to the fibrils as the transmitting parts. But the work of such histologists as Boveri (1886) on the structure of the nodes of Ranvier did not support the opinion of Bethe, nor did this opinion seem tenable to more recent students of the subject (von Lenhossék, 1910). Hence Bethe's second effort to prove that neurofibrils are the conductors of the nervous system failed to be convincing (Ramón y Cajal, 1903a, 1906a).

### ARE NEUROFIBRILS ARTEFACTS?

In a cursory survey of the work on neurofibrils covering the ninety years that have elapsed since their discovery it must be evident that students of these structures have come to rely more and more on complicated and intricate methods for the demonstration of these bodies. The discoverer Remak claimed that he saw these fibrils best in fresh cells and fibers. Schultze, their chief advocate, described them from fresh tissue or from that examined in serum. Then came the attempts of Frommann and of Kupffer to stain the fibrils specifically, followed by the brilliant but precarious method of Apáthy, which gave way to the rather intricate but reliable means of demonstration devised by Bielschowsky, Ramón y Cajal, and Bethe. But any one who has worked even with these more recent

methods must have been impressed with their precariousness (Legendre, 1906b, 1907a, 1907b). Tello (1922), using the Ramón y Cajal procedure, was able to demonstrate a fibrillar system in connective tissue cells as well as in nerve cells. All workers were familiar with the fact that different preparations made by the same method commonly show great differences in the details of the fibrils and even in the same preparation the fibrils of different parts differ greatly among themselves. This diversity of appearance has been made the subject of critical comment by Clivio (1927), and is the chief basis for that skeptical attitude that many modern workers maintain toward the whole problem. Thus Bayliss (1914) in his *Principles of General Physiology* expressed the opinion that the so-called neurofibrils are pure artefacts produced by the methods employed in the histological preparation of the nervous tissue in which they are seen and that they are in no sense constituents of the living cell. This opinion had also been entertained by Pighini (1908) and Auerbach (1911a, 1911b, 1912). W. H. Lewis and M. R. Lewis (1924, p. 403), both experienced cytologists, reached much the same conclusion. Cowdry (1928, p. 972) on the other hand, after admitting the great uncertainty that is to be attributed to the methods by which neurofibrils have been demonstrated, remarks that these bodies must have some material basis in the cell and that they cannot be due altogether to technique. Somewhat the same opinion as Cowdry's was expressed by Boeke (1926), who admitted the existence of neurofibrils in living tissue but in forms other than those seen in preparations. The ease and quickness with which they disintegrate were emphasized by Marinesco (1914).

A solution for these difficulties is not easily found. The fact that neurofibrils can be demonstrated by a great variety of methods is not conclusive proof, as some have thought, that these bodies are constituents of living cells, for all such methods involve coagulation. Nor does the demonstration of neurofibrils in tissue instantly killed in hot water (Lugaro, 1909) show that the fibrils were present before the killing. In fact no evidence is conclusive on this point except that which can be drawn from living material. What can be demonstrated in the living cell is surely there. Much of the evidence from living cells dates from the time of Remak and Schultze, though fibrils were later identified under the ordinary microscope by Nansen (1887) and under the polarizer by Göthlin (1913). Within the last two years, however, a very important addition to this body of fact has been made by Bozler (1927b).

### THE WORK OF BOZLER

This investigator has shown that in the large living nerve cells in the circular nerve band of the jellyfish *Rhizostoma* it is possible to demonstrate with remarkable clearness a system of neurofibrils. These fibrils run lengthwise in the bipolar cells that make up the subepithelial nervous tissue in this creature. When this animal is placed in slightly hypertonic seawater, its nerve cells, in consequence of the general shrinkage of its tissues, shorten and thus throw the bundles of contained neurofibrils into folds (Fig. 8). Under such circumstances the neurofibrils, often partly isolated, can be seen with great clearness in the cells, and yet in this state the tissue is still living, for the jellyfish as a whole continues to pulse and on being returned to ordinary sea water it makes a complete recovery.

Another remarkable fact noted by Bozler (1927b, p. 260) is that after *Rhizos-*

*toma* has been for some time in hypertonic seawater small hernia-like enlargements appear on the surfaces of its nerve cells (Fig. 9). These sacs are formed in consequence of pressure adjustments and each sac remains attached to its cell by a very narrow neck. Into the cavity of such a sac is squeezed not only some of the fluid neuroplasm from the nerve cell but also portions of its neurofibrils, which fold and bend upon themselves in such a way as to demonstrate in a most conclusive fashion their complete integrity and independence. It would be difficult to devise a more satisfactory demonstration for neurofibrils as real structures in living nerve cells than this is, for the cells are living and the fibrils are observed under these circumstances and without hardening or staining.

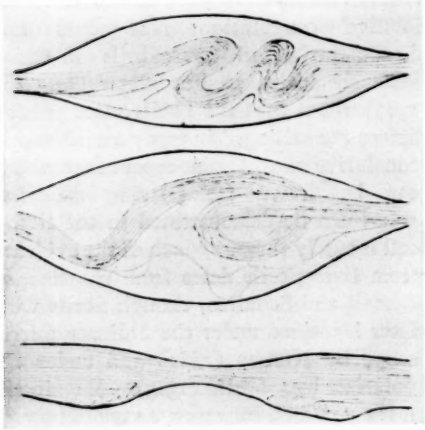

FIG. 8. LIVING NEURITES IN THE JELLYFISH RHIZOSTOMA WHICH HAD BEEN SUBJECTED TO HYPERTONIC SEAWATER; IN CONSEQUENCE OF THIS TREATMENT THE NEUROFIBRILS ARE MUCH FOLDED

Bozler, 1927b, p. 259, Abb. 2

Evidence of this kind points to the correctness of the original observations by Remak and by Schultze and renders it impossible to deny the existence of neurofibrils as constituents of living nerve cells. Incidentally it may be mentioned that although Bozler was the first to call attention in a critical way to the neurofibrils of *Rhizostoma*, these bodies had already been noticed many years earlier in the living tissues of this jellyfish by Hesse (1895).

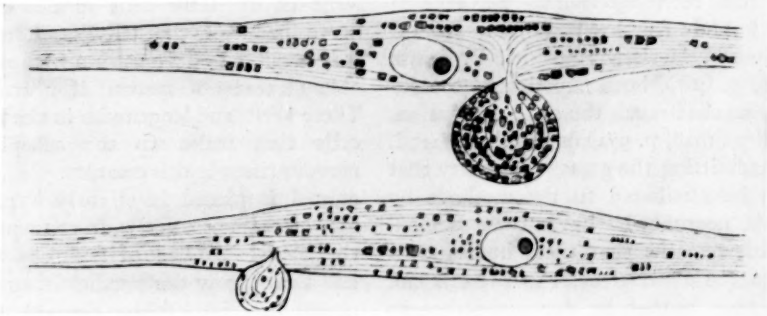

FIG. 9. LIVING BIPOLAR NERVE CELLS FROM THE JELLYFISH RHIZOSTOMA WHICH HAD BEEN SUBJECTED TO HYPERTONIC SEAWATER; AS A RESULT OF THIS TREATMENT THERE HAVE FORMED ON THE CELLS SMALL HERNIA-LIKE ENLARGEMENTS INTO WHICH THE NEUROPLASM AND ITS CONTAINED GLOBULES HAVE FLOWED AND THE NEUROFIBRILS HAVE BENT

Bozler, 1927b, p. 261, Abb. 3

### THE STRUCTURE OF NERVE FIBERS

Bozler's work is not only important in indicating what neurofibrils are, but it

yields very significant results on the general problem of the physical conditions of the materials contained within ganglion cells and nerve fibers. Aside from minute particles such as mitochondria and the like, the cytoplasm of nerve fibers and ganglion cells contains in the main two materials, neurofibrillar substance and the intervening neuroplasm or interfibrillar material as it is sometimes called. The older cytologists held a variety of opinions concerning the physical properties of these materials. According to Koelliker (1896), Retzius (1889) and others, neurofibrils are filaments of the consistency of a fairly firm gel imbedded in a firm neuroplasm. Thus the whole axis cylinder of a nerve fiber was believed by this school to be relatively resistant, a condition that was supposed to be characteristic of the substance of the nerve cell also. According to another group of workers, represented by such investigators as Leydig (1857) and Nansen (1887), the neuroplasm of cells and fibers was looked upon as a firm material through which the neurofibrils extend as fluid-filled tubules. From this standpoint neurofibrils are not firm bodies but cavities in a matrix of stiff jelly. Finally a third school, composed of many investigators including Kupffer (1883), Boveri (1886) and others, claimed that neurofibrils are relatively tough filaments in a fluid neuroplasm. It is difficult to harmonize the observations of Bozler with the opinions of any of these groups except the third. The formation and filling of hernia-like sacs and the folding of neurofibrils into such sacs, as clearly shown in Bozler's figures, are conditions hardly to be understood except on the assumption of a fluid neuroplasm and a relatively resistant neurofibril. Such an interpretation of the physical condition of these elements is quite in agreement with the observations of Matsumoto (1920) on the movement of small bodies, such as mitochondria, in the neuroplasm of growing axis cylinders and with those of Ingvar (1923) on the shifting of the whole neurofibrillar framework through the neuroplasm of centrifuged nerve cells. These and other like observations show beyond a doubt the correctness of the growing conclusion among neurologists that the neuroplasm of nerve cells and of nerve fibers is a fluid in which relatively firm neurofibrils are suspended.

Although the work on living nerve cells compels us to admit that neurofibrils are real constituents of these bodies, it does not oblige us to accept as such all the structural features that have been ascribed to these fibrils by past workers. Most of these features have been described from specially prepared material, and as already pointed out there is no certainty that they may not be the results of the methods of preparation. Before such features can be accepted they must be demonstrated in the living cell.

From what is known of neurofibrils in the living state it may be said that they are relatively firm filaments that form axial systems of parallel members in nerve fibers and complicated intermeshing feltworks in cell bodies. They apparently do not divide, nor do they extend beyond the limits of the nerve cell in which they originate. Whether they anastomose and form true networks or not is a question that cannot at present be answered. Such unions were not observed by Bozler (1927a, p. 257) in *Rhizostoma*, where, had they been present, they might easily have been seen. At the moment little more can be said with certainty about the structure of neurofibrils. New discoveries concerning them must await the finding of especially favorable material and the application of novel methods for the

study of this material in the living condition.

### WHAT IS THE FUNCTION OF NEUROFIBRILS?

In passing from the structural aspect of neurofibrils to their functional side we leave a region in which the light, though dim, is certain for a field of almost complete obscurity. Most of the neurofibrillists, and this includes such vigorous advocates as Apáthy (1899) and Bethe, accepted Max Schultze's dictum that neurofibrils are the transmitting elements of the nervous system. This opinion is almost universal, for only a few workers have expressed other views. Thus von Lenhossék (1910), without, however, denying that neurofibrils may play a part in conduction, regards them as primarily concerned with the mechanics of early development and ascribes to them what might be called a supporting function in the progressive growth of the axis cylinder. That the neurofibrils constitute a purely sustentative system internally bracing the external form of the neurone is the opinion of Koltzoff (1906, 1912), Goldschmidt (1910) and von Szüts (1914a), who in this respect stand out in strong contrast with most other neurofibrillists (Apáthy, 1907b; Bethe, 1913).

It is true that neurofibrils are firmer in texture than the neuroplasm that fills much of the space in the nerve cell, but it is also true, as Bozler, (1927b, p. 258) has pointed out, that this extra firmness is so slight as to be of no real value in forming a skeletal organelle. This conclusion is well supported not only by Bozler's own experimental evidence but also by such observations as those of Ingvar (1923), according to whom the whole fibrillar system of a nerve cell may be broken down by centrifugation without seriously disturbing the form of the cell itself. Thus there seems to be no good reason for assuming that neurofibrils are primarily supporting elements. The neurone maintains its shape chiefly through its outer covering and not in consequence of an inner skeleton.

Having reached this point in his discussion of the function of neurofibrils Bozler (1927b, p. 262) ends by stating that since neurofibrils are not sustentative they must by process of exclusion be conductors. This conclusion would be sound if it could be shown that these two functions exhaust the list of possible neurofibrillar activities. But, it may be asked, are there not other possible functions for neurofibrils than mechanical support and nervous conduction?

As intimated at the beginning of this section there is at present almost no real evidence on which to base a conclusion concerning neurofibrillar activities. At best hypotheses may be framed to which future work may or may not give support. To this category belong the opinions already briefly outlined. They may be designated the conduction hypothesis of Schultze, the histogenetic-sustentative hypothesis of von Lenhossék, and the pure sustentative hypothesis of Koltzoff and Goldschmidt. In this list belongs also the proposition with which this paper closes.

### A METABOLIC HYPOTHESIS OF THE NEUROFIBRIL

The life of the neurone is a complex one. In consequence of its function of conducting nerve impulses this type of cell has developed enormously attenuated processes which in the form of nerve fibers penetrate the animal body often for great distances. In man, for instance, some of these fibers have a length of a meter or more, while their diameters may be only five thousandths of a millimeter or about the thickness of a cobweb. A fiber of approxi-

mately such a diameter and one meter in length is 200,000 times as long as it is thick. This delicate strand is kept alive throughout its whole extent by its connection with the cell body, whose nucleus is in some way essential to its continued life, for should it be cut through anywhere the part thus separated from the nucleated portion quickly degenerates and dies. This metabolic activity over an enormously attenuated thread is maintained in all nerve cells that they may continue to carry out their very important function of conduction.

The motor fibers of the higher animals transmit certainly two and perhaps three sets of independent influences. First of these is the influence that excites activity in a muscle and that is ordinarily spoken of as the nerve impulse. It passes over these fibers at a relatively high rate, exhibits the all-or-none principle, and is the nervous activity that has been studied for a century or more by workers in the field of nerve-and-muscle physiology. There also pass outward over every motor fiber those influences mentioned in the last paragraph, that are conducive to growth and repair and that are essential for the continued life of every part of the neurone. These metabolic influences emanate from the nucleated portion of the cell and pass to the uttermost ends of the neuronic processes. Finally motor nerves transmit impulses that excite in muscles not momentary activity but that mild continuous contraction, the so-called state of tonus. What these influences are has been scarcely more than guessed at, but that they are different from the other two types is not improbable. They may, however, depend upon a separate innervation from that concerned with ordinary motivity, in which case we are justified in ascribing to any one class of motor fibers not more than two sets of transmitted influences (compare Hardy, 1927).

Two of these three possible sets of influences, the ordinary nerve impulses and the metabolic influences, are recognizable in the sensory neurone, where the independence of these influences is clearly shown by the difference in the direction of their conduction. On the distal stretch of an ordinary sensory neurone in the vertebrates the nerve impulses run toward the central organ, while the metabolic influences run away from it. Hence these two activities must be admitted to be separate.

What parts of the neurone are concerned with these two types of conduction? A final answer to this question cannot be given, but a certain amount of evidence is beginning to appear. It is coming to be a recognized fact, as Hanström has recently noted (1928, p. 481), that the nucleated part of the neurone is its trophic or metabolic center.

From this center, as already pointed out, emanate influences that are essential for the continued life of the whole neurone. This nucleated center is what was designated as the ganglion cell by the older neurologists, and by many of them such cells were supposed to be the seat of the central nervous functions. For years this has been a current opinion, but there is as a matter of fact not the least evidence in favor of it (Nansen, 1887; Bethe, 1904; Parker, 1918). In many instances, such as the bipolar sensory neurones of the lower vertebrates or the bipolar elements in *Rhizostoma*, as recently described by Bozler, the nucleated part of the neurone lies in the line of nervous transmission. But in a number of other cases, as in the unipolar neurones in higher vertebrates and in some invertebrates, the nucleated portion of the neurone is well to one side of the tract of neuronic nervous transmission. In some of these instances the cell body is attached to this tract by only a slender protoplasmic neck. In this type of

neurone the courses taken by the nervous impulses and by the metabolic influences are believed on good grounds to be distinctly different. In the ordinary sensory neurones of vertebrates the nerve impulses originate at the peripheral end, make their way centrally over the neurite, and, without entering the body of the cell, pass on to discharge at the central end of the neurone. The metabolic influences on the other hand originate in the region of the nucleus of the cell body, pass down its neck to the tract of nervous transmission where they separate into two streams, one flowing peripherally over the neurite and the other centrally over the central nerve-fiber process.

This conception of the transmission systems within the neurone is favored by the small amount of experimental evidence that has thus far been brought forward. Bethe (1897, p. 629; 1898b) in his study of the nervous system of the crab *Carcinus* showed that the unipolar cell bodies of a group of neurones in the brain of this animal could be removed without disturbing the reflexes of the second antenna, the muscles of which were innervated by these particular neurones. Hence it may be legitimately concluded, as is implied in the preceding consideration, that the cell bodies of many neurones are not traversed by the nerve impulses but that these impulses take a direct course from the receptive to the discharging end of the element concerned.

If, however, we follow the course of the neurofibrillar tracts within such neurones we find them far from agreeing with those of the nerve impulses. The fibrillar tracts occupy the axes of the neurites but at the junction of the neurite with the unipolar cell process they turn into that process and after passing through it, invade the cell body forming extensive whorls around its nucleus. Or, reversing the description, it may be said that the bundles of neurofibrils start from the region of the neuronic nucleus, pass down the unipolar neck of the cell body and spread from that neck distally and proximally over the fibers of the neurone to their terminations.

Thus the course of the neurofibrils does not follow that of the nerve impulses but does duplicate exactly that of the metabolic influences. I conclude therefore that the neurofibrillar system in the neurone is concerned specifically with the distribution of the metabolic influences and not with the conduction of nerve impulses. These influences start in the region of the neuronic nucleus and spread over the lines of neurofibrils throughout the whole neurone. What the metabolic influences are it is impossible at present to say. It seems hardly reasonable to think of them as streams of material in the nature of a hormone, emanating from the region of the nucleus and percolating throughout the neurone. Such a passage of material might however occur over interfacial boundaries as already suggested for the true nerve impulse by Brinkman and Szent-Györgyi (1923). Or they may be chains of ionic readjustment such as have been proposed as an explanation of the nerve impulse. But however we consider them, the hypothesis here put forward assumes that they are what the neurofibrils transmit. This hypothesis further assumes that the neurofibrils are not concerned with the transmission of the nerve impulse, as asserted by Schultze and advocated by Apáthy and Bethe, nor with the mechanical support of the neurone as maintained by Koltzoff and Goldschmidt and in a qualified way by von Lenhossék.

If nerve impulses are not transmitted by neurofibrils what part of the neurone does transmit them? Von Lenhossék (1910) was probably correct in declaring that no

specific part of such a cell can be singled out for this special activity. The transmission of nerve impulses, according to him, is rather a function of the neurone as a whole, than of any of its parts. And yet certain of these parts are probably more intimately concerned with this operation than others are. The growing belief as to the nature of the nerve impulse is that it is a progressive wave of ionic readjustment in some membranous layer of the neurone (Lillie, 1923). Where this layer is located is not easily determined, but that it is about the surface of the neurone is much more probable than that it is buried in its depths. The periphery of the axis cylinder is a much more probable location than the core of that structure. It is well known that if we estimate the metabolism of nerve fibers by the carbon dioxide they give out and designate the amount of this gas discharged by a given quantity of quiescent fiber in a given time as 100 per cent, the increase due to the passage of nerve impulses in the active state of the fiber is only some 15 per cent (Parker, 1928). These relations are not inconsistent with the belief that the core of the fiber is concerned with maintaining a state of responsiveness on the surface by which the fiber on stimulation is enabled to transmit impulses and to recover from the effects of such transmission. From this standpoint the core of the axis cylinder is believed to be concerned chiefly with metabolic activities, the periphery with transmission. While this statement is a pure assumption there are no facts so far as I am aware that prevent its acceptance.

The hypothesis that neurofibrils are the parts of the neurone especially concerned with the metabolism of its more distant parts is not only supported by the distribution of these fibrils within the neurone but also by their course of development. It will be remembered that two important facts stand out in the developmental history of the neurofibrils: first, that their initial appearance is in close proximity to the neuronic nucleus and, second, that they develop while the neuroblast is gradually changing into a neurone and some time before nervous functional activity has appeared. Both these facts are without special meaning if we assume neurofibrils to be conductors of nerve impulses, but both are significant if we believe the fibrils to be concerned with metabolic influences, for these influences emanate from the nucleus and must be of first importance in the early stages of neuronic growth and before nervous activity has begun. Thus the little that is known of neurofibrillar development favors the hypothesis set forth in this paper rather than that of nervous conduction.

The idea that the neurofibrillar system of the nerve cell is a part of the metabolic outfit of the neurone is avowedly hypothetical and yet as an hypothesis it meets at present more of the known facts about the neurone than the hypotheses of nervous conduction or of support appear to do. Hence comes the justification of its presentation, in full understanding that its worth will be determined as our knowledge of the neurone increases.

### POSTSCRIPT

In addition to the fibrillar systems in nerve cells there are two other sets of fibrils that call for some consideration. These are the fibrils in the cells of many ciliated epithelia and in the cells of certain protozoans. In both instances these systems have been interpreted as means of controlling the beat of the cilia or other like parts on the given cells.

The fibrillar system in ciliated epithelia

has been recently studied with much care by Grave and Schmitt (1925), who have shown, for instance, that in cells from the foot of the mollusk *Lampsilis* a fan-shaped system of converging fibrils occurs, the spread ends of which are in contact with the basal bodies of the cilia and the converging ends of which terminate in the deeper part of the cell close to the nucleus (Fig. 10). These fibrils, which

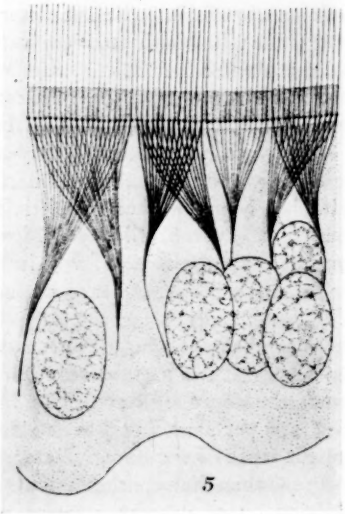


FIG. 10. CILIATED EPITHELIUM FROM THE FOOT OF THE MOLLUSK LAMPSILIS SHOWING FAN-SHAPED BUNDLES OF FIBRILS EXTENDING FROM NEAR THE NUCLEUS OF THE CELL TO THE BASES OF THE CILIA

Grave and Schmitt, 1925, p. 513, Fig. 5

were long ago described in other similar cells, are believed by Grave and Schmitt to be the means of regulating the metachronous beat of the cilia. But this beat passes over the whole ciliary field without reference to cell limits and it is therefore difficult to understand how such a distinctly cellular mechanism as this is could serve as a regulator of such an activity. On the other hand a comparison between the nerve cell with its neurofibrillar system leading from near its nucleus to its peripheral parts and the ciliated cell with a fibrillar system that also starts from close to its nucleus and extends to the basal ends of the cilia is highly suggestive. It is quite possible, judging from the connections shown in the ciliated cell, that its fibrillar system is in reality a counterpart of that already described for the nerve cell. The nucleus of the ciliated cell is without doubt its metabolic center and the cilia are obviously the parts that would call most heavily on the metabolic resources of the cell. Are not the fibrils, then, that lead from the region of the nucleus to the cilia the most probable parts to be concerned with this transfer of resources? With this view in mind a comparison between them and the neurofibrils of nerve cells seems reasonable.

A second system of fibrils that has recently attracted the interest of investigators is that contained in the cell bodies of certain protozoans. These fibrils have been claimed to constitute what has been called a neuromotor system and the function ascribed to them has been the conductive activities in the control of the cilia, commonly the specialized cilia, of these protozoan cells. From this standpoint they were studied first by Sharp (1914) and later by Yocom (1918), Kofoid and Swezy (1919), Taylor (1920), McDonald (1922), Rees (1921, 1922), and Vissher (1927). All these workers have interpreted the fibrils as parts of a neuromotor system. It has, however, been pointed out that they may serve as a purely supporting mechanism. In *Euplotes* (Yocom, 1918; Taylor, 1920) *Trichomitus* (Kofoid and Swezy, 1919) and *Paramecium* (Rees, 1921, 1922) the systems from the cilia concentrate on a center that is in close proximity to the nucleus, a condition that favors the

extension of the hypothesis advanced in this paper for the fibrils in nerve cells and in ciliated cells to those in the protozoan cell. It must be remembered, however, that in two protozoans, *Diplodinum* (Sharp, 1914) and *Balantidium* (McDonald, 1922), systems of fibrils have been described concentrating on a so-called motorium not located near the nucleus. It is, however, possible that these systems may be something other than those described for *Euplotes*, *Trichomitus*, and *Paramecium*, in which the nuclear relations are most obvious. It would be difficult to imagine a system better placed for the transfer of metabolic influences from the nucleus to the cilia than that described by Rees for *Paramecium* (Fig. 11), and when it is remembered that, as Jennings and Jamieson (1902) long ago showed, fragments of *Paramecium* continue to exhibit essentially normal ciliary activity for many hours after they have been prepared, it would seem likely that the fibrillar system in this protozoan was more concerned with some such function as that ascribed to it in the present paper than with the immediate control of the ciliary beat.

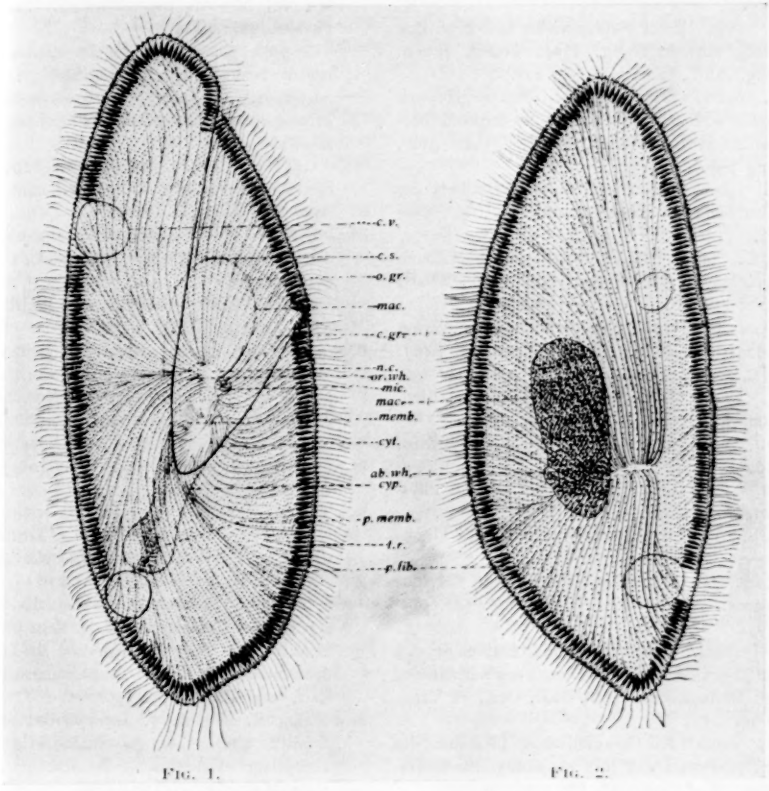


FIG. 11. SEMIDIAGRAMMATIC SKETCH OF THE SYSTEM OF FIBRILS IN PARAMECIUM

Rees, 1921, p. 465; *mac*, macronucleus, toward which the fibrils concentrate on both the oral (Fig. 1) and the aboral side (Fig. 2) of the protozoan.

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# A CENTURY OF STUDY UPON THE DEVELOPMENT OF THE EUTHERIAN VENA CAVA INFERIOR

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ONE hundred years ago, Karl Ernst von Baer published the first part of his monumental work: *Ueber Entwickelungsgeschichte der Thiere; Beobachtung und Reflexion.* For many structures this great work serves as the classic foundation of modern embryological study, and of the veins this might especially be said. It would seem fitting and proper, after a century has elapsed, that we pause to take stock of what has been accomplished. Concerning the veins we may say this: the time is ripe for an assessment of the literature, with a view to determining what it contains of permanent value. The majority of opinions entertained by former observers, especially with regard to the vena cava inferior, obviously cannot continue indefinitely to receive mention by those who essay to present historical introductions along with their supposedly new opinions apropos of that vein. Out of respect for past investigators and for the convenience of future readers, it is desirable that the elimination of what is thought to be irrelevant be carried out justly, and that credit for discovery be bestowed where it belongs. So far as the inferior vena cava is concerned, it must be admitted that our progress has not been such that we are able to look back from the goal of ultimate truth and presume to say who has deviated least from the path leading to it. For just now the confusion is greater than it has ever been except, perhaps, during the year 1888.

Modern methods and appliances have, however, advanced to such an extent that the problems of the veins do at least lend themselves to solution. Technique has been evolved which might conceivably enable us to produce accounts complete enough for all practical purposes and graphic expression. On the purely material side there is hope. But, the trend of Anatomy being what it is, well may we wonder whether the lure of Physiology will leave among us those with training and fortitude sufficient to the adequate disposal of the problems of venous development. Among many writers of textbooks of Embryology, to say nothing of the students of that subject, there exists a feeling of genuine aversion towards further progress in the study of veins if that is to involve greater intricacy and detail than existing accounts would indicate. Doubtless this difficulty with regard to the veins might be overcome if we were to produce a really complete account, place it safely in our archives, then prescribe for the unwilling student a diluted dose of venous embryology.

Whether we are in the throes of the final act, or whether the year 1928 merely sees us entering, with misgivings, into a second century of work upon venous development, it is well at this auspicious time to segregate and to summarize a few of those expressed opinions concern-

ing the truth of which we may feel relatively sure.

### PERIODS IN THE STUDY OF THE VASCULAR SYSTEM

Definite eras through which the study of the vascular system has passed may be significantly associated with certain vogues of technique. The great classical work upon the development of the vascular system may be said to have been ushered in with the nineteenth century. The previous century had brought about advances in the study of comparative anatomy. Cuvier and Meckel were the leaders of such study in the early part of the nineteenth century. Of the study of the embryology of the vascular system, von Baer and Rathke were the great pioneers. They, like their predecessors, depended largely upon the direct observation of the living embryo, relatively fresh material, or the dissection of preserved material. Wolff, Malpighi, Haller, Hunter, Spallanzani, Döllinger, Pander, Gruithuisen, Kaltenbrunner, and others had examined and figured the living blastoderms, studied the vascularization of the embryonic membranes, the developing vessels in transparent portions of larval amphibia and various fishes, the more superficial intraembryonic vessels, circulation in the external gills, and the heart; the latter structure was a favorite object for early investigations.

An extensive review of the early nineteenth century work upon the origin of endothelium is given by Allen Thomson (1832). Near the year 1815 there was controversy over this subject, perhaps less intense but equally intelligent as that which subsided in 1915. Among the names recorded in Thomson's discussion are those of the most eminent anatomists of that time.

The era of von Baer and Rathke (which I shall arbitrarily term the "classical period") is characterized by figures in which the vessels are shown in their original relations to accurately drawn neighboring structures—veritable direct illustrations of embryonic bodies, parts, or dissections. This era extended to about the year 1840. Inadequate microscopical equipment and a shortage of closely graded material offset to an extent the advantages of skill and of the remarkable capacity for accurate observation possessed by these great investigators.

Then followed some forty years of relative inactivity. There is no better way of determining the situation in anatomy at that time than to consult the indices of the *Archiv für Anatomie und Physiologie* of the period. Anatomists had turned to physiology and to chemistry. The period was characterized by what Professor E. G. Conklin (*Science*, vol. 68, no. 1768) has most aptly called 'frantic physiology.' But with the popularization of the serial section and later the wax reconstruction there came, for the embryology of the vascular system, a renaissance in which His and Hochstetter may be regarded as the great leaders. The period is preeminently that of figures and diagrams of models of the larger vascular trunks removed from their topographical relationships with other structures. The method lent itself to the study of deep vessels which had never been seen by direct observation. The twentieth century, that of recent study, has seen a refinement of the technique of sectioning and reconstruction, as well as a revival of the injection method. The latter had been used occasionally upon foetal and embryonic material by such early workers as John Hunter, Huschke, and von Baer.

Modern investigators have succeeded in rediscovering a number of facts recorded in the classical accounts long since forgotten; and they have been not entirely

reluctant to accept discoverers' credit for the restatement of that which had already been thought to be true. Recent investigators have been content to restate the reviews written toward the end of the nineteenth century. American observers especially, for want of libraries containing the earlier literature, have often had to give their assent to previous reviews and have often merely cited those references which had obviously not been available for direct perusal. Thus it is that certain misconceptions have come to be regarded as historical facts. Our perspective for the study of veins is incomparably worse than it is for most embryological study. Modern investigators have failed particularly to appreciate the amount of information possessed by von Baer and by Rathke with regard to embryonic capillary plexuses generally, and the development of the cranial vessels and dural sinuses specifically. (Consult especially Rathke (1839, p. 111) on the direct protracted observation of the capillaries of the brain wall of the living snake embryo and his studies of the venous sinuses of the head.)

### THE WORK OF KERSCHNER

In the present account it will be possible to treat of only a few details of early work upon the development of veins of the dorsal body wall. In any serious attempt to determine the proper use of the terms *Vena cava inferior* and *V. cardinalis posterior*, it is necessary to consider the historical relationships of these two terms. Certain value was evidently attached by Hochstetter to the historical account given by Kerschner (1888-a). Many valuable references cited by Kerschner appear in the discussion by Hochstetter (1893), who concurs (*ibid.*, p. 611) with Kerschner (1888-a, p. 812) that the work of Stark (1835) probably influenced Rathke (1838) to abandon certain notions of the vena cava which he had entertained in 1830. Lewis (1902) depended in part upon Hochstetter's (1893) review. Huntington and McClure (1920) refer to the work of Hochstetter and Rathke as being fully appreciated by them. Butler (1927, p. 269) shares the view of Kerschner concerning the influence of Stark upon Rathke. Sabin's (1915) review of the literature of vena cava is manifestly based upon Kerschner, whose statement of the problem as a whole is accepted by Sabin. Butler's review (1927) reiterates many of the statements of Hochstetter (1893) and several which Sabin had based upon Kerschner, and recommends Kerschner's review as a source of valuable information. There is thus a definite tendency to depend upon Kerschner for our perspective. If we accept the statements of that author, then the personality of Stark bulks large in the history of our knowledge of the vena cava. It can be shown, however, that many of the statements of Kerschner are not to be taken seriously. Hochstetter (1888-a) has demonstrated this to an extent. In turn, Sabin's presentation of Kerschner's views is in some ways unreliable, and is particularly misleading, insofar as it gives the impression that Kerschner offered a correct interpretation of the inferior vena cava. For the author who attempts it, the task of unravelling all this confusion is not a profitable one, nor would a complete survey of the historical facts be the most pleasant subject-matter possible for the consideration of those persons who cannot endure the spectacle of authors expressing opposite opinions enthusiastically. Yet we may certainly say that if distorted or inadequate reviews have been thought worth the printing, then additional effort is warranted in the elimination of confusion

which these reviews have occasioned, and those authors who have contributed to the confusion should be the last to complain.

I propose to review first the accounts of Kerschner (1888-a and -b) in relation to the work of Hochstetter (1887, 1888-a, -b, 1893, and 1902); in relation to the work of Rathke and Stark; and in relation to recent work. The contributions of the early authors may then be considered in relation to each other. The announced purpose of Kerschner's first article (1888-a) on the morphology of the V. cava inferior is that of determining an anatomical and embryological basis for interpreting certain venous anomalies. The greater part of the discussion is occupied with refuting the conclusions of Hochstetter (1887).

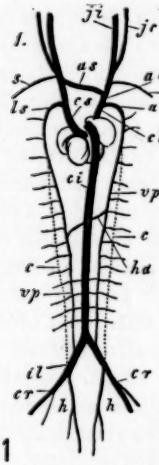
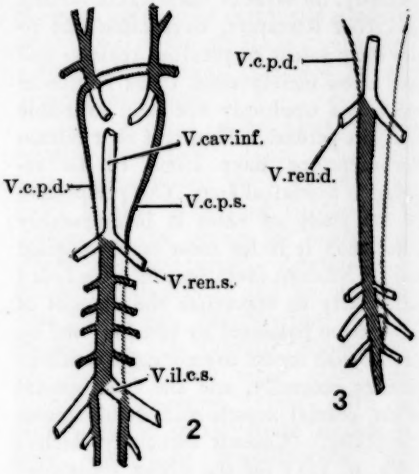



FIG. 1. SCHEMA TO REPRESENT THE DEVELOPMENT OF THE SYSTEM OF SUPERIOR AND INFERIOR CAVAL VEINS

(From figure 276, p. 404, Kölliker's *Grundriss der Entw. des Menschen u. der höheren Tiere* (1884).) *c*, "obliterated middle portion of the cardinal veins"; *vp*, "newly developed 'posterior vertebral' veins, forming new portions of the azygos and hemiazygos lines and receiving lumbar and intercostal veins." For the explanation of the remainder of the labelling consult the original. The figure is obviously based upon Rathke's description (1838).

THE WORK OF HOCHSTETTER

For a period of some fifty years prior to the work just mentioned, writers of embryological text books had generally accepted the notion of Rathke (1838) that the azygos veins (largely) and the postrenal V. cava (entirely) are new formations independent of the cardinal veins. Diagrams similar to those of Gegenbaur (1870), Henle-Krause (1876), and Kölliker (1884) served to explain the developmental process (consult my figure 1). Hochstetter's (1887-a) diagrams showed V. azygos and V. cava inferior as cardinal derivatives. Elaborations of these latter figures are



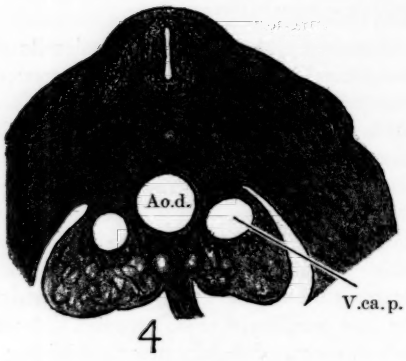

FIGS. 2 AND 3. DIAGRAMS TO REPRESENT THE FORMATION OF THE POSTRENAL V. CAVA IN MAN (2), AND IN THE RABBIT (3)

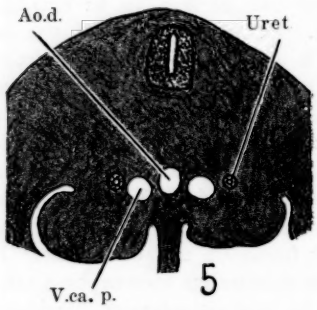
(From Hochstetter 1887, p. 518.) According to this schema, the V. cava inferior and the azygos and hemiazygos veins are directly derived from posterior cardinal veins. It was from these diagrams that Hertwig executed his figures on p. 537 of his *Entwicklungsgeschichte des Menschen und der Thiere*, 5te Aufl. The latter diagrams are copied in many recent textbooks. They are often represented as being derived from the figures of Hochstetter. Not only are they inadequate to illustrate Hochstetter's views, but they fail to portray conditions even remotely resembling those in any mammal. Minot (1898) called attention to their inadequacy.

those employed in most of the recent embryological text books (consult my figures 2 and 3). Kerschner (1888-a) contended that these latter diagrams of Hochstetter were incorrect, and that even if they were correct, the notion which they illustrate was not original with Hochstetter, but that they represent a theory of venous development expounded by Rathke (1830-a); that Rathke had abandoned this theory, influenced probably by the work of Stark (1835). Kerschner pointed out (as noted by Sabin) that the V. cava lies medial to the kidney, whereas the cardinal vein of Rathke lies lateral to it. Hochstetter replied (1888-a) to this criticism as follows:

> that his view was neither a confirmation of the earlier (1830-a) nor the later (1838) view of Rathke; that Rathke (1830) had merely followed the current practice of designating as "hintere Hohlvenen" two large posterior vessels in plain view for direct observation (this being the means of study at Rathke's disposal); that these "hintere Hohlvenen" are "was wir heute *hintere Cardinalvenen* nennen;" that the right "hintere Hohlvene" of Rathke (1830) in its totality could not possibly become V. cava; that Kerschner was oblivious to the possibility (as supposed by Hochstetter) that Rathke could not have seen the posterior cardinal veins in their mesonephric segments; that whereas Rathke (1830-a) describes "zwei einander höchst ähnliche Gefässe 'deren jedes an der äusseren Seite der beiden falschen Nieren,' von hinten nach vorn verlauft," the cardinal veins (according to Hochstetter, 1888-a, p. 871) "liegen nun bei Säugetierembryonen nie an der äusseren Seite der Urnieren —" but dorsomedial to it from the time of their first appearance; that the mesonephric sections of these vessels could therefore not have been observed by Rathke, who consequently "die Hohlvenenentwickelung zweimal in verschiedener Weise unrichtig beschrieben hat;" that the mammalian postrenal V. cava inferior lies upon the dorsomedial border of the mesonephros throughout the existence of that organ and that its position at all times "vollständig mit der rechten hinteren Cardinalvenen übereinstimmt;" that Kerschner had merely consulted a certain amount of literature and had given play to his imagination. It is from the store of knowledge of V. cava possessed by Hochstetter in 1887 (represented usually by Hertwig's diagrams) that most modern text books of embryology have acquired the material for their accounts of that vessel.

We need not enter into the details of Kerschner's (1888-b) reply to Hochstetter, but preferably we may note the advance made by the latter observer (1888-b) in his article dealing with the influence of the permanent kidney upon the development of the veins. This appeared simultaneously with Kerschner's reply. From this article (Hochstetter, 1888-b) one learns that the series of embryos which he had previously (1887) studied did not afford stages of development exhibiting a venous "island" in which the permanent kidney can be seen to be encircled by veins. For the history of the subject this is an admission, the importance of which deserves emphasis. Hochstetter's accounts (1887 and 1888-b) present differences practically as great as those of the accounts by Rathke (1830-a and 1838). His statement (1888-a), already quoted, to the effect that the posterior cardinal is never found on the dorsolateral border of the mammalian mesonephros can in no way be harmonized with his description of the original posterior cardinal line as given in his later account (1888-b). In this connection consult my figure 6. In younger stages he had apparently noted conditions similar to those seen in figure 4. In older stages he had probably noted conditions seen in my figure 5. His greatest error was to suppose (1888-a) that the dorsal aorta is a reliable landmark by which to establish the identities of vessels lateral to its postrenal segment in two somewhat separated stages of development. When he had acquired sufficient material upon which to make a more complete study (1888-b), he found conditions similar to those in figure 6. On pages 939 and 940 of the latter account he stated that the more lateral vessel involved in this "island-formation" (consult figures



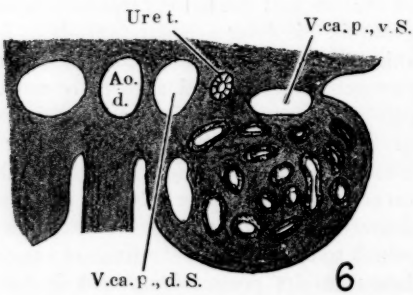




FIG. 4. CROSS-SECTION THROUGH THE MESONEPHROI OF A 13-DAY RABBIT EMBRYO SHOWING CORRECTLY THE ORIGINAL RELATION OF POSTERIOR CARDINAL VEIN TO MESONEPHROS

(After Hochstetter, 1888-b, p. 939, figure 1.) *Ao*, aorta, *V.ca.p.*, vena cardinalis posterior.

FIG. 5. CROSS-SECTION THROUGH THE POSTRENAL MESONEPHRIC SEGMENT OF THE INFERIOR V. CAVA OF A 15-DAY RABBIT EMBRYO

(From Hochstetter, 1888-b.) The Anlage of V. cava of the region is labelled *V.ca.p.* (V. cardinalis posterior). In 1887, Hochstetter erroneously considered such vessels as *V.ca.p.* in figures 4 and 5 to be identical structures. *Uret.*, ureter.

FIG. 6. CROSS-SECTION THROUGH THE MID-LUMBAR REGION OF A RABBIT EMBRYO, SECOND HALF OF THE FOURTEENTH DAY

(Copied from Hochstetter, 1893, *Tafel* 22, figure 14.) This shows Hochstetter's later interpretation of posterior cardinal vein (*V.ca.p.*, *v.s.*) in relation to a newly-established 'Collateralvenenbahn' (*V.ca. p.*, *d.s.*) which forms the mid-lumbar portion of V. cava. These two vessels are described as ventral and dorsal "Schenkeln" of a "Cardinalveneninsel." The "ventral Schenkel" represents the *V.ca.p.* of figure 4. The "dorsal Schenkel" really represents the *V.ca.p.* of figure 5.

6 and 7) was a segment of the original posterior cardinal vein which had been pushed aside and compressed dorso-ventrally by the "migrating" kidney; that this pressure had not only displaced the posterior cardinal, but had interfered with the flow of blood in it; that as a consequence there developed (in the rabbit) a new vein taking exit from the posterior cardinal at the level of the caudal end of the kidney and reentering that vessel at the cranial end of the kidney; that the original cardinal line so involved rapidly degenerated, while the new vessel, designated by Hochstetter as a new "collateral Venenbahn" rapidly increased in size to form postrenal vena cava of the region. Summarizing this, he stated:

> Es hat sich also in Urnierabschnitt der hinteren Cardinalvene jederseits eine Insel gebildet, in welche die Anlage der bleibenden Niere gewissermassen hineingesteckt erscheint. Der dorsal Schenkel dieser Insel nimmt nun die gleich Lage zur Aorta ein wie früher die Cardinalvene *selbst*.

The term "periureteric venous ring of Hochstetter" as employed by recent authors is a misonomer. He used no such term. The statement of the fundamental problem (by Kerschner and by Sabin) as being involved in the question whether a vessel lateral to the kidney could ever become vena cava might imply this: that authors who claimed vena cava to be of posterior cardinal origin must have be-

lieved vena cava to form lateral to the kidney. Neither in his earlier nor his later work did Hochstetter express such a belief.

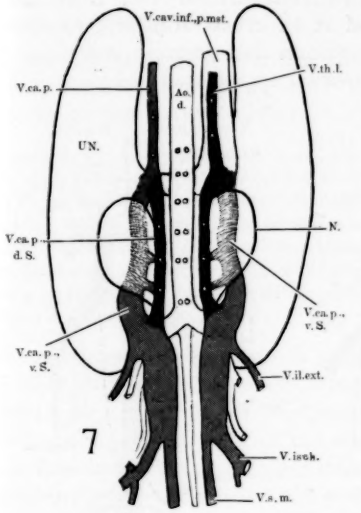



FIG. 7. MESONEPHROS, KIDNEY, AORTA, AND V. CAVA INFERIOR OF A RABBIT EMBRYO AT THE MIDDLE OF THE 14TH DAY ILLUSTRATING THE "CARDINALVENENINSEL" IN RELATION TO THE URETER

(Modified from Hochstetter, figure 19, *Tafel* 23, 1893.) On the left side of the figure, the venous path regarded by Hochstetter as being derived from the original posterior cardinal line is shaded by diagonal lines. The new "dorsal Schenkel" of the "Insel" is shown in solid black. The present writer has taken liberty to modify the right side of the figure to the extent of showing the prerenal *V.ca.p.* of the original as a new formation labelled *V. thl.* according to a suggested usage (Reagan, 1927-b). The parts of the "Cardinalveneninsel" are labelled in accordance with the usage in the preceding figure. *A.i.e.* and *V.i.e.*, "internal iliac" vessels. *V.i.*, ischiadic vein. *A.s.m.* and *V.s.m.*, medial sacral vessels. *U.N.*, mesonephros. *N.*, metanephros and ureter.

Hochstetter has remained reluctant to apply a new and specific embryological term to the above-described "collateral Venenbahn" which contributes to postrenal vena cava. Much less has he seen fit to apply to it a term dissociated from the term *cardinal vein*. The nearest approach to a specific embryological term for it, in Hochstetter's usage, is "dorsal Schenkel" of the "Cardinalveneninsel." On the contrary he was willing to apply to the "ventral Schenkel" of the "Cardinalveneninsel" a specific term not involving the concept of "cardinal." I

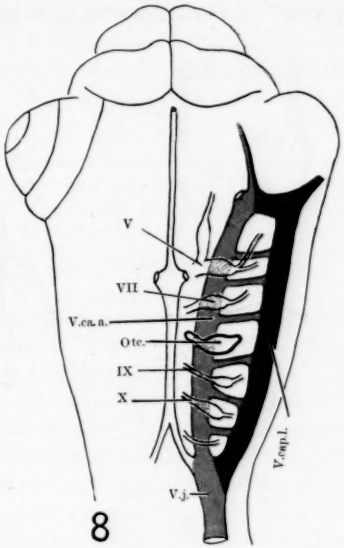



FIG. 8. DIAGRAM OF THE HEAD-DRAINAGE IN RELATION TO THE CRANIAL GANGLIA OF TROPIDONOTUS

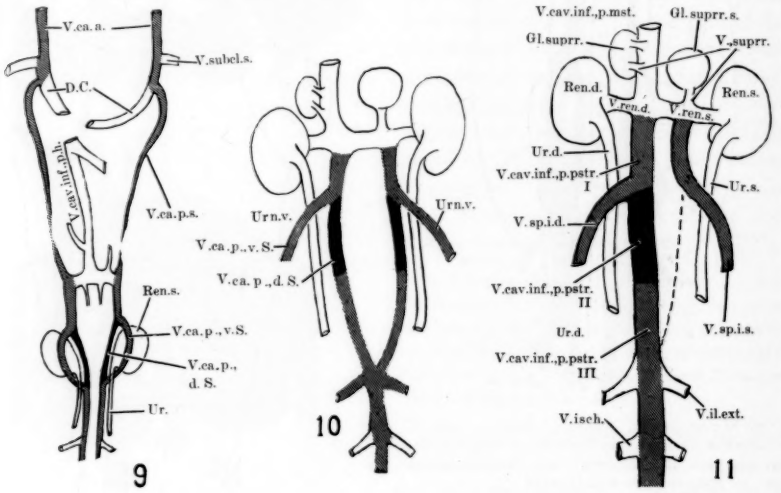
(From Hochstetter, 1902, figure 152, p. 133 in Hertwig's *Handbuch*, based upon Grosser and Brezina.) In effect, an anterior "Cardinalveneninsel" is here represented. The new "Collateralvenenbahn" properly receives the specific designation *V. capitis lateralis* (*V. cap. l.*) not involving the overworked term *cardinal*, while the latter is reserved for the original "Schenkel" of the "Insel." The cranial ganglia are indicated by Roman numerals. *Otc.*, otocyst. *v.j.*, vena jugularis.

refer to his term "Urnierenvene" which he applied (1893) to a derivative of the original cardinal vein. In general, this usage was carried out in Hochstetter's account in 1902. In the latter account his attitude toward the question of specific terminology for elements of an "island-formation" permits of much clearer description for the cranial region than for

the abdominal region. On page 133 (*ibid.*) he gives a figure of "island-formation" as it takes place in the anterior cardinal vein of *Tropidonotus*. Here, in contrast with his usage for the posterior cardinal (consult my figure 8) he retains the term "anterior cardinal" for that "Schenkel" of the "Insel" which represents the original anterior cardinal line; for the newly established "collateral Venenbahn" he makes use of the specific, non-cardinal embryological term *Vena capitis lateralis*. Toward clarity of description this is a distinct advance. It would be unfortunate if no system of terminology comparable to this were ever permitted for the veins of the thoracic and lumbar regions.

For the original vascular path medial to the cranial ganglia the term *v. capitis medialis* had been in frequent use. For it, Sabin (1917) suggested the etymologically impossible substitute *Vasa primitiva*.

From a program of work so epoch-making and extensive as that which Hochstetter carried out, it is difficult, and at all events arbitrary, to select for discussion his greatest individual contribution to the study of veins. In this connection, his figures 14 and 19 of his *Tafel* 22 are of outstanding importance (consult my figures 6 and 7). So far as I am aware, these are the first figures ever published showing coexistent anlagen of mammalian postrenal vena cava along with the original mesonephric sections of the posterior cardinal veins. I can find no evidence, either by way of illustration or discussion, that any predecessor of Hochstetter ever saw the true forerunner of postrenal vena cava and mesonephric




FIGS. 9, 10, AND 11. DIAGRAMS TO ILLUSTRATE THE FORMATION OF THE V. CAVA INFERIOR IN THE RABBIT

(Modified from Hochstetter, 1902, in Hertwig's *Handbuch*, p. 142, figures 166–168.) In the original figures all veins are shown in solid black. Attempt is made here to indicate the derivatives of the original cardinal veins by lighter shading. For explanation of labelling, consult the preceding figures. *Ur.*, ureter. *V.ca.p.*, posterior cardinal vein. *V.sp.i.*, vena spermatica interna. *V.c.i.*, vena cava inferior, postrenal section. In the original of fig. 9 the veins which have more recently been called "subcardinals" were designated by Hochstetter as "Urnierenvenen." In 1893 he had used the latter term to designate the cranial remnants of the "ventral *Schenkeln*" of his "Cardinalveneninseln." In figure 10, the latter usage has been substituted.

posterior cardinal as parallel, coexistent structures in any individual mammalian embryo.

### SABIN'S INTERPRETATION OF RATHKE AND KERSCHNER

On page 27, Sabin (1915) makes this statement, which I can regard only as being without foundation of fact:

> Rathke, however, in his subsequent work, published in 1838, gave up the theory that the lower segment of the inferior vena cava came from the posterior cardinal vein, because he had specimens in which two vessels were present, namely a vessel medial to the kidney, making the anlage of the vena cava, and a vessel lateral to the kidney or the posterior cardinal vein (see Kerschner, p. 812).

Without success may one search page 812 of Kerschner (1888-a) for any statement lending itself to such an interpretation. The same may be said of the entirety of Kerschner's writings. Not once did Kerschner state that Rathke had seen both the above-mentioned vessels (as we know them at present) coexistent in the same mammalian embryo. The preparation of Kerschner's account preceded the publication of that of Hochstetter (1888-b) in which the latter observer mentioned for the first time his mammalian "Cardinalveneninsel." Again on page 27 (1915) Sabin states:

> In 1888 Kerschner analyzed the views of Rathke and Hochstetter and concluded that the lower segment of the inferior vena cava could not be a transformed posterior cardinal vein for two reasons: first, the vena cava has a position more mesial and more ventral than the posterior cardinal ever has; and secondly, at a certain stage both veins are present in the same specimen. This sums up the whole question . . . . .

I have searched every page ever written by Rathke upon the development of the venous system. I find no evidence that he ever saw "both veins present in the same specimen" of a mammalian embryo. Let us now consider Kerschner's interpretations. In the first place, if (as quoted from Sabin) Kerschner stated that the postrenal part of V. cava has a position more *ventral* than the posterior cardinal ever has, that alone should arouse our suspicion of Kerschner's incompetence to "sum up the whole question" of the development of the V. cava. The weakness of Kerschner's argument did not remain unnoticed by Hochstetter. On pages 871–2 (1888-a) the latter discusses the point:

> K. folgert dann weiter: "Ein medial und ventral von den Urnieren (den Nieren) gelagerte Gefäss kann der Cardinalvene nicht entsprechen." Woher Herr K. die Kentniss über eine so eigentümliche Lage der hinteren Hohlvene hat, ist mir ziemlich rätselhaft geblieben . . .

Hochstetter then stated that the anlage of postrenal V. cava is always *dorsal* and medial to the right mesonephros. Evidently his objection to Kerschner's description had to do with the supposed ventral position of the vein with reference to the mesonephros. Sabin (1915, p. 25) quotes exactly the same lines from Kerschner's account (1888-a, p. 813) and pronounces his statement to be "entirely correct." We have, then, a situation requiring to be explained.

### WHAT DID KERSCHNER MEAN?

After much careful study of the writing of Kerschner, I have with some hesitancy come to the conclusion that he supposed the right revehent mesonephric vein (early *right inferior subcardinal* of F. T. Lewis and more recent authors) to be the anlage of normal postrenal V. cava of the ordinary eutherian mammal. If this conclusion be justified, then Kerschner, at least, was probably influenced by Stark.

Kerschner's central purpose (1888-a) was avowedly the interpretation of the more common type of anomalous "doubling" of the postrenal V. cava. He had

evidently found an instance of "hohe Teilung" of the vein, in which the left homologue of normal postrenal V. cava had persisted parallel to the normal vessel. In terms of this he attempted to interpret what he could find in the literature upon the developmental process involved. Taking this anomaly as a point of departure, he stated (*loc. cit.*, p. 815) that normal postrenal V. cava is a unilateral product of bilateral anlagen; that two bilaterally homologous longitudinal anlagen are united by two transverse anastomoses; that one of these anastomoses occurs at the renal level, forming the left renal vein; that the other normally occurs at the level of the lower limbs; that if the latter anastomosis fails to form, a "left inferior V. cava" joins the right at the renal level; that these postrenal bifurcations (roots of the V. cava) are comparable to attenuated Vv. iliacae communae. On page 819 (*ibid.*) Kerschner defines the term "iliac vein" as he uses that term for mammals, and as he claims it was used by Rathke and by Nicolai. He says this vein consists developmentally of two parts: a lateral portion formed from the anastomosis between posterior cardinal and the root (*Wurzelast*) of the vena cava (subcardinal-postcardinal anastomosis of recent authors), and a longitudinal part, the root of the vena cava itself. He states that this is not Hochstetter's use of the term iliac. On page 815 Kerschner (1888-a) concludes "dass die Vv. iliacae primitivae der Vogel den beiden Wurzeln einer gedoppelten Cava, also den wirklich 'verlängerten' Vv. iliacae comm. gleich zu setzen sind." He also states on the same page that the terms for the parts of the cava of birds are directly applicable to the cava of mammals, this statement follows those concerning the "doubled" cava of mammals. He states on the same page that the Venae renales revehentes of reptiles and amphibians correspond to the Vv. iliacae of birds. If, therefore, as stated by Kerschner (1888-a, p. 815) the normal "double" V. cava of the seal, or the abnormal double V. cava which he attempted to interpret involved a persistence of the left homologue of normal postrenal V. cava (which he would regard as the left "root of the V. cava"), it follows that he derived normal typical eutherian postrenal V. cava from the mammalian homologue of the right revehent mesonephric vein of the anamnia. The early revehent mesonephric veins of anamnia were termed "subcardinal veins" by F. T. Lewis in 1904 (consult my figures 12 and 13). Von Baer and Rathke frequently called the caudal portions of the revehent mesonephric veins of lower vertebrates "roots of the V. cava." Hochstetter, Kerschner, Balfour, Minot, and many others called the mammalian homologues of the caudal portions of these revehent vessels "roots of the V. cava." Lewis (1902) called these "roots of the V. cava" of mammals "inferior divisions of subcardinal veins" in the youngest stages figured by him.

We have noted the claim of Sabin to the effect that Kerschner correctly interpreted mammalian postrenal vena cava on the basis of these propositions: that postrenal vena cava and posterior cardinal vein coexist in the same specimen, separated from each other by the kidney, in such arrangement that vena cava is on the medial side of the kidney, while posterior cardinal is lateral to it; that Kerschner derived this notion from Rathke and Hochstetter. It is clear that if this were true, Kerschner must have believed in something at least faintly resembling the "Cardinalveneninsel" of Hochstetter. Hochstetter's discovery of his mammalian "Insel" had, however, not been published prior to the time of Kerschner's account.

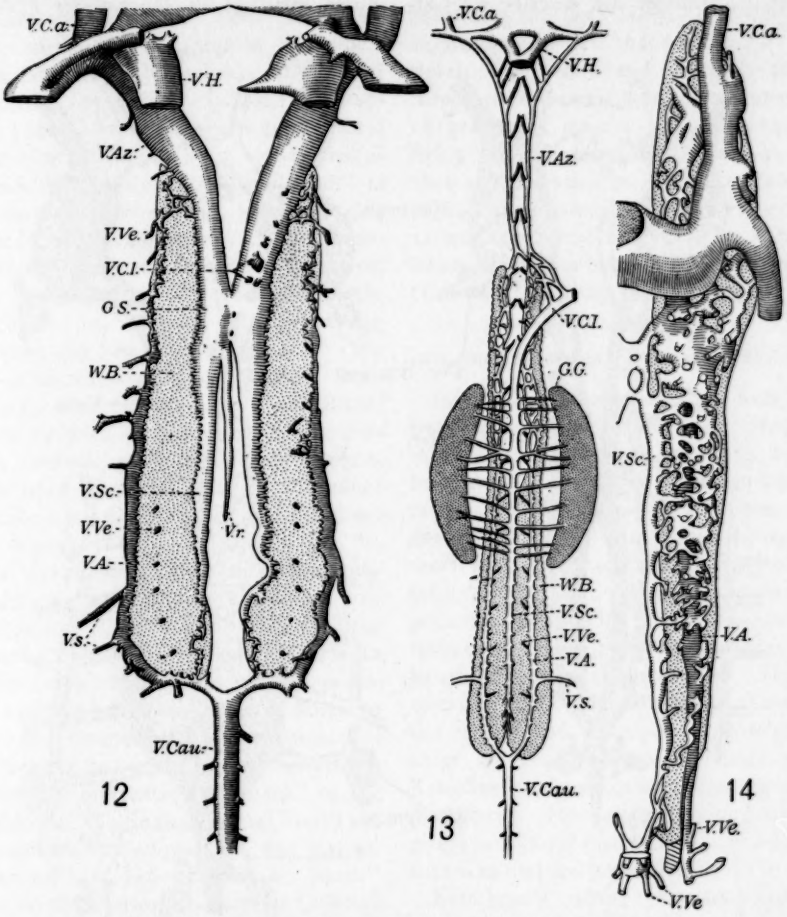



FIG. 12. RECONSTRUCTION OF THE VEINS OF A 51-MM TORPEDO EMBRYO

(After F. T. Lewis, 1904, figure 6, p. 268.) *V.C.I.*, vena cava inferior. *V.Az.*, "mesonephric azygos vein" (renal portal vein; advehent mesonephric vein of Hochstetter; posterior cardinal vein). *V.Sc.*, "subcardinal vein" (revehent mesonephric vein of Hochstetter, 1892, Taf. 17, figure 9). *V.H.*, hepatic vein. *V.r.*, vein from rectal gland. *G.S.*, genital sinus. *W.B.*, Wolffian body.

FIG. 13. INJECTION OF THE VEINS IN AN ADULT NECTURUS PREPARED BY THE LATE PROFESSOR PRENTISS

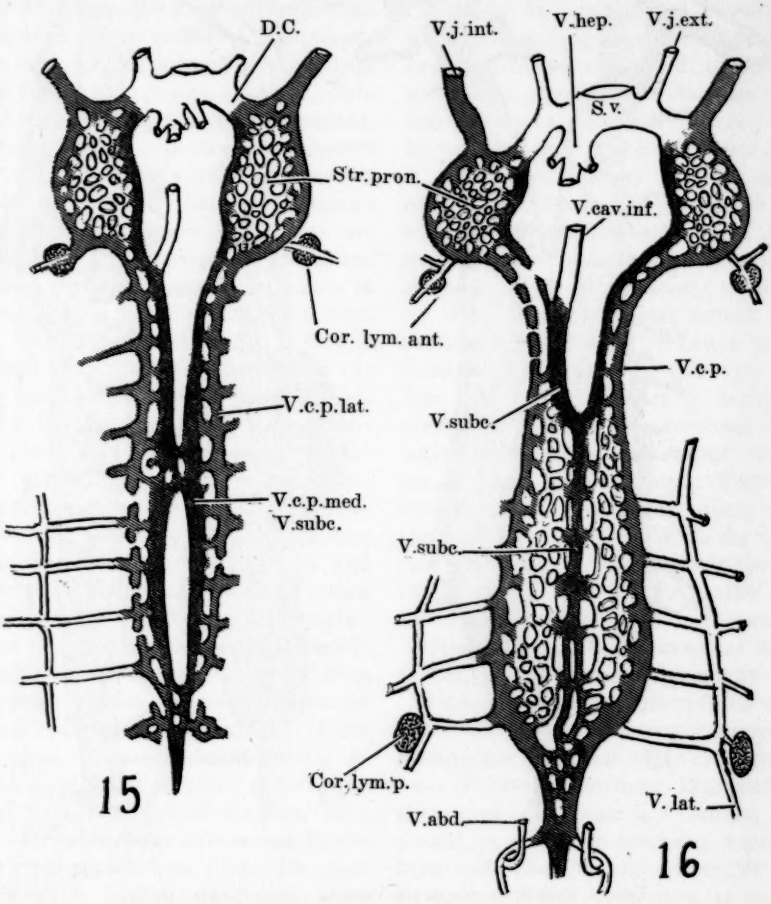
(After F. T. Lewis, 1904, figure 7.) *V.Ve.*, vertebral vein. *G.G.*, genital gland. *V.s.*, somatic vein. (Other abbreviations as in figure 9.)

FIG. 14. RECONSTRUCTION OF THE NETWORK OF SINUSOIDS IN THE LEFT WOLFFIAN BODY OF A 5 MM. LACERTA

(After F. T. Lewis, 1904, figure 8.) Compare with figures 12 and 13, and with Hochstetter, 1892. For explanation of the labelling, consult the two preceding figures.

Turning to pages 821–823 (1888-a) we find that Kerschner did describe a "Car-

In connection with the "Insel" the previous writings of Hochstetter (1888-c)




FIGS. 15 AND 16. RECONSTRUCTIONS OF THE VEINS OF BUFO VULGARIS AND B. LENTIGINOSUS, RESPECTIVELY 7 AND 15 MM

(After Kampmeier, figures 3 and 5, pp. 88 and 89, 1920.) In figure 15, the revehent mesonephric vein (here called medial part of posterior cardinal vein) is well formed (*V.c.p., med.*), while the advehent mesonephric vein (here called lateral portion of the posterior cardinal vein) is only in the process of formation as fusions between adjacent intersegmental tributaries to the more medial vein. Compare with F. T. Lewis (1904), figure 5. In figure 16, the revehent mesonephric veins are called "subcardinal" while the advehent ones (*V.c.p., lat.*) are called posterior cardinal. For abbreviations and fuller explanation consult the original figures.

dinalveneninsel" with coexistent medial and lateral "Schenkeln." The "Schenkeln" lie on opposite sides of the kidney.

and of Rathke are discussed. Unfortunately the animal in which Kerschner's "Insel" is discussed is an amphibian,

whose kidney, needless to say, is not a metanephros. It therefore possesses no post-metanephric V. cava such as mammals have. As stated by Kerschner, in description of his schema, the lateral "Schenkel" of this last-discussed (amphibian) "Insel" is the advehent mesonephric (posterior cardinal) vein. The medial "Schenkel" of his amphibian "Insel" is the revehent mesonephric vein (*loc. cit.*, p. 821). Kerschner (alluding to the amphibian "Cardinalveneninsel") states on this same page: "Der rechte mediale Schenkel . . . . stellt die Fortsetzung der Cava dar (die meisten Säuger)." He derives his schema of "Inselbildung" from the figures of Goette (1875) and Hochstetter (1888-c) on amphibians. Kerschner's (1888-a, p. 823) final pronouncement upon Hochstetter is to the effect that the latter (in his mammalian studies) had mistaken the "Wurzeläste der V. Cava" (revehent mesonephric veins, comparable to the "mediale Schenkeln" of amphibian "Cardinalveneninseln") for posterior cardinal veins, and that Hochstetter (1887) had either ignored posterior cardinal veins themselves or failed to see them. In effect, Kerschner claims that Hochstetter had confused the mammalian homologue of medial "Schenkel" of the amphibian "Cardinalveneninsel" with the mammalian homologue of the lateral "Schenkel" of the amphibian "Insel." As a matter of fact Hochstetter (1887-a) had confused the medial "Schenkel" of his later-to-be-discovered mammalian "Cardinalveneninsel" (fig. 5, *V. ca. p.*) with the potential lateral "Schenkel" (fig. 4, *V. ca. p.*) of that "Insel." Kerschner did not know that the amphibian and the mammalian "Inseln" involve totally different medially located structures; invariably he erroneously supposed that mammalian mesonephros and metanephros have identical topographical values for the interpretation of veins. Where he used topographically the term *Urniere*, he (see my p. 187) inserted parenthetically the term *Niere*. Not only did he erroneously state that postrenal V. cava develops medially and ventrally to the mesonephros as well as to the metanephros (a statement quoted and approved by Sabin), but he also stated (1888-a, p. 813) that the mammalian posterior cardinal vein is dorsolateral to the metanephros as well as to the mesonephros. This is likewise far from being "entirely correct." (Compare Sabin, 1915, p. 25.)

### OUR DEBT TO HOCHSTETTER AND KERSCHNER

In 1888 both Hochstetter and Kerschner performed genuine service in reviving our interest in the subject of vena cava, and in bringing to light much forgotten history of the study of veins. At the time, each author combined with youthful enthusiasm an inadequate understanding of the subject. At first, Kerschner apparently possessed the wider knowledge of the literature. Hochstetter's knowledge was based upon original observation. He had certainly not availed himself of the existing figures and descriptions of relationships of the posterior cardinal vein. Kerschner wielded his language as a sharp instrument. Hochstetter wielded his language as a blunt instrument. The literature was decidedly enriched.

Kerschner's short articles contain several examples of brilliant reasoning. In one of the best, he states (1888-a, pp. 811–812):

> Auch lassen sich gewichtige Grunde der menschlichen und vergleichenden Anatomie dafür anführen, dass wir Anastomosen-systems längs des Sympathicus je nach der medialen oder lateralen Lagerung zu demselben abermals in zwei verschiedene Ketten zerlegen müssen. Ganz unaufgeklärt ist schliesslich der Wechsel der Lagebeziehung der Cardinal- und Vertebralvenen zur Aorta und zum Sympathicus, der selbst im Beckenabschnitt eine Lageänderung sein dürfte.

At their own loss, subsequent observers have ignored this useful suggestion. (By vertebral veins, the "posterior vertebral veins of Rathke" are implied).

Kerschner pointed out (1888-a, p. 810) the fact (as shown in figures by Haller, 1756) that a portion of the V. azygos reaches to a level decidedly caudal to the renal anastomosis, and thus accompanies a portion of the postrenal V. cava before joining it; that Hochstetter's diagrams (1887-a) failed to explain this fact.

That the human V. azygos anastomoses with V. cava inferior well below the renal level is a familiar fact of ordinary anatomical description. Figures by Poirier and Charpy, Testut, Lazar (Anatomical Plates), and Robinson (1891) show this caudal connection. Yet the later stages of development of this part of V. azygos are explained away by Hochstetter (1902), McClure and Butler (1925), and Butler (1927), either by hiatuses in the figures or by series of dotted lines in that location indicating atrophy of the azygos lines prerenally.

Hochstetter's diagrams (1902, p. 142; see my figure 9) make no provision for the condition pointed out by Kerschner, though his description (1893) of a new part of the V. azygos helps to explain it. Kerschner (1888-a, p. 817) correctly followed certain predecessors when he self-contradictingly stated that for the revehent mesonephric veins of anamnia, the terms *cardinal vein* (equivalent to posterior cardinal of recent authors) and *posterior vena cava* (of earlier authors) served "eben so gut und eben so schlecht."

Although Kerschner (1888-a, p. 820) stated that his views were not in conflict with those of Rathke (1838), Kerschner believed in a "paired anlage" of postrenal V. cava, whereas Rathke (1838) described for it an "unpaired anlage." On page 809 (1888-a) Kerschner noted that many diagrams then in use (see my figure 1) made no provision for the anomalous "doubling" of the postrenal V. cava, though, unlike the diagrams (see fig. 2) by Hochstetter (1887-a), they showed it to be a new formation. Kerschner reviewed the opinion of Krause (1876) that the "superfluous left-sided postrenal V. cava" is a serial continuation and homologue of V. hemiazygos. Kerschner stated his belief that this temporary left lumbar caval vessel was a bilateral homologue of normal postrenal V. cava. On the basis of this, he suggested (p. 809) that normal postrenal V. cava is a serial homologue and continuation of the "vertebral" (non-posterior-cardinal) part of V. azygos. This hitherto unemphasized fact of history is of interest in connection with the theory developed subsequent to Kerschner's account, by Huntington and McClure, Sabin, and Butler.

Removed from context, many statements of Kerschner are quite impressive. For instance, on page 814 (1888-a) he states that so far as their original embryonic plexiform condition permits, V. cardinalis posterior and the anlage of postrenal V. cava inferior are independent structures. The lustre of this remark is dulled by the fact that Kerschner did not even know an anlage of postrenal V. cava when he saw it or, perhaps more correctly, he did not know when he was not seeing one. F. T. Lewis (1902) makes no mention of Kerschner, but on page 241 Lewis makes this significant statement:

It has been the custom of certain embryologists to give the name of the whole of the vena cava to one of its parts, namely the subcardinal portion, and even to charge with ignorance those who called other sections of the adult vessel the vena cava.

Undoubtedly the recent tendency has been to accord Kerschner too important a place in the history of the subject, and to misrepresent the views of Hochstetter or to minimize the importance of them.

MISINTERPRETATIONS OF HOCHSTETTER'S VIEWS

On page 236 (1902) F. T. Lewis states that the permanent kidney, coming into contact with the cardinal, may "split" that vessel "to form a loop as figured by Hochstetter." On page 270, Butler (1927) represents Hochstetter as believing that

> the location of the adult vena cava medial to the right kidney and ureter came about by a split in the posterior cardinal vein; this gave rise to a periureteric ring, the lateral half of which was lost, while the medial half persisted to form the main channel.

We have already seen (p. 184) that in one account (1888-b, pp. 939–940), Hochstetter recognized the ventrolateral "Schenkel" of the "Cardinalveneninsel" as the original posterior cardinal vein (*selbst*), and the dorsomedial "Schenkel" as a new "collateral Venenbahn." In his *Bemerkungen zu Zumstein's Arbeit*, Hochstetter (1898, p. 516) makes this statement, which I quote without comment:

> Zumstein beschreibt ferner für denselben Embryo das Auftreten einer Spaltung in der hinteren Kardinalvene, die zur Inselbildung in dieser Vene führen soll. Leider hat Zumstein wieder nicht angegeben wie er sich diese Spaltung in der Kardinalvene zustände kommend denkt und warum er meine Angaben, welche die Bildung der Insel in den hinteren Kardinalvenen einer die segmentalen Venen dieser Gegend in Verbindung setzenden kollateralen Venenbahn entstehen lässt, für unrichtig ansieht. Denn wenn an allen den von ihm untersuchten Embryonen, wie er sagt, der dorsale Schenkel der Insel schon vollständig zu sehen ist, so beweist dies doch durchaus nicht, dass erstens die Insel durch Spaltung der ursprünglich einheitlichen Kardinalvenenbahn entsteht und zweitens, dass ihr dorsaler Schenkel nicht der Ausbildung einer Kollateralen Venenbahn seine Entstehung verdankt.

On page 239 (1902) F. T. Lewis points out an error made by Kollman, who, presumably basing his account on Hochstetter, describes the hepatic part of V. cava as uniting directly with the posterior cardinal vein. Lewis states that "in this he follows Hochstetter's earlier description (1893, p. 569)." Sabin (1915, p. 27) states that Lewis cleared up the existing confusion by showing that the hepatic part of vena cava does not unite directly with the posterior cardinal; that this is the fundamental contribution of Lewis. Again we do well to consult Hochstetter. On page 515 (1898) he states that the hepatic part of vena cava applies itself to the ventral surface of the Wolffian body, a relationship said by Hochstetter (*loc. cit.*) to have been made clear in his account in 1893, but to have been ignored by Zumstein (1898). Hochstetter (1898, p. 515) states:

> Soll die so gelagerte V. cava mit der rechten V. cardinalis, die an der Dorsalseite der Urniere verlauft, in Verbindung treten, so kann dies nur durch ein Venenrohr geschehen, welches von der Cava winkelig abbiegend an der medialen Fläche der Urniere vorbei in die V. cardinalis posterior übergeht. Diese rechtwinkelig auf V. cava und V. cardinalis posterior verlaufende Verbindung ist in meiner Fig. 9 (*Tafel* 21, 1893) aufs deutlichste zu sehen.

On page 569 (1893) his description is not contradictory to the view just quoted. Not only does he describe one large anastomosing vessel (comparable to the subcardinal-posterior cardinal anastomosis of recent authors) at right angles to "vena cava" and posterior cardinal, but he describes several smaller ones said to be reminiscent of the mesonephric drainages from renal portal veins of birds and reptiles (small subcardinal-postcardinal anastomoses of recent authors). Again the inadequacy of his account is largely a matter of terminology. Here he obviously "applied the term for the whole of the vena cava to one of its parts, namely the subcardinal portion," a practice concerning which I have already quoted the comment of Lewis.

Hochstetter's observations have swept wide horizons. Often his most important

conclusions are very briefly and casually stated. His work contains great funds of information practically unexplored by recent authors. His short controversial articles are in some ways the most instructive. Much unprofitable future discussion could be avoided in the literature relating to veins, if those of us who are still novices upon the subject were required to read and to cross-index every page of Hochstetter before giving forth our own nascent opinions.

### THE WORK OF RATHKE

We may now consider the work of Rathke. In addition to providing information upon points in the work of Rathke which have ordinarily been neglected, I shall attempt to afford answers to these questions which are at once raised if we wish to harmonize the contents of previous reviews with the present review:

(1) Was Rathke (1830-a) so ill-informed as to suppose that the mammalian postrenal vena cava develops lateral to the permanent kidney? (2) Was he unaware that a part of V. cava inferior traverses the liver, and if not, did he believe that a part of the posterior cardinal vein becomes incorporated into the liver? (3) Was the work of Stark the first to set forth correctly the relation of V. cava to kidney and liver? (4) Is there any real evidence that Rathke was influenced by Stark? (5) Was the view of Hochstetter (1887-a) identical with that of Rathke (1830)? (6) Is Rathke's final interpretation reconcilable with that of Kerschner?

I find negative answers to all these questions. Hochstetter answers the fifth negatively. In all other cases where the points are discussed at all, these questions are answered affirmatively in the reviews of Hochstetter, Kerschner, Sabin, and Butler.

Whereas in 1830 Rathke did apply the term "hintere Hohlvenen" to the vessels which we now call posterior cardinal veins, and emphasized the fact of their position dorsal and lateral to the mesonephroi, he certainly was aware that postrenal vena cava (see my figures 26 and 27) lies medial to the kidney. On page 69 (*ibid.*) he stated that his account was only a preliminary one, and that a more complete one was to follow it. In 1830 he barely indicated the main points as he understood them:

that the mesonephric segment of the right "hintere Hohlvene" (posterior cardinal of later authors) undergoes a migration (*Wanderung*) from the dorsolateral side of the mesonephros to the dorsomedial border of that structure and to a position close to the dorsal aorta; that this migration takes place earlier in the cranial part of the mesenophros than in the caudal part; that the mesonephros becomes displaced laterally with the growth of the kidney; that, as a result of the medial migration of the right "hintere Hohlvene," that vessel comes to lie close to the left mesonephros; that as a consequence a venous anastomosis between the two mesonephroi is more readily possible (*loc. cit.*, p. 68) "als wenn jener Venenbahn um seinem ursprünglichen Ort verharrt wäre." He states (p. 69, *ibid.*) that along with this venous cross anastomosis there appear as branches of the transverse anastomosis, two longitudinal vessels on the ventromedial surface of the left mesonephros, the cranial one being in direct line with the caudal one; that "zwei ähnliche Aeste ubrigens verbinden auch die rechte falsche Niere mit der bleibenden hinteren Hohlvene." (These may represent the revehent mesonephric veins and the hepatic anastomosis). Regardless of the fact that in one part of his account he stated that the vessel which we now call right posterior cardinal is the "nachherige hintere Hohlvene," he was probably referring to that part of "bleibenden Hohlvene" located in (what we now call) caval mesentery, rather than to posterior cardinal vein when he stated that the veins upon the ventral surface of the right mesonephros "verbinden sich auch die rechte falsche Niere mit der bleibenden Hohlvene." A vessel on the ventral surface of the mesonephros is obviously not in position to unite that structure with a vessel in the position to which Rathke had described the (vessel which we now call) posterior cardinal as having migrated. It is also very significant that Rathke did not state that the caudal part of the vessel ventral to the right mesonephros formed postrenal V. cava. He states that the portion of the left "hintere Hohlvene" lying in the abdominal region degenerates. The later work announced as a completion of this tentative sketch

appeared in 1832. I can find nothing in Rathke's account in 1830 which would lead one to assume either that he was ignorant of the existence of the hepatic part of V. cava, or that he supposed the vessel which we now call posterior cardinal vein could ever become incorporated into the liver. He showed the latter vessel (see figure 24) well removed from the liver.

However disappointing the present-day reader may find Rathke's (1830-a) account just discussed, he is likely to experience genuine surprise at the accuracy of Rathke's (1832) badly neglected accounts of the dorsal body wall veins, especially in the lower vertebrates; here there is almost complete lack of confusion, owing largely to Rathke's employment of the relatively reliable and safe terms *advehent* and *revehent veins* of the embryonic excretory system.

Rathke (1832 and 1839) frequently refers to "the advehent and the revehent veins of Jacobson." In the writings of Jacobson (1815 and 1817) to which I have had access, the terms "advehent and revehent" veins of the embryonic excretory system do not appear. The renal portal veins (advehent mesonephric veins of Rathke) are referred to by Jacobson (1817, p. 148) as the *Vv. renales inferiores;* the revehent mesonephric veins of Rathke (early subcardinals of F. T. Lewis) are called *Vv. abdominales anteriores*, by Jacobson. The latter has often been given credit for the discovery of the revehent mesonephric veins. Also the advehent mesonephric veins (amphibian posterior cardinals) are often called "veins of Jacobson."

In Rathke's account of these veins in reptiles (1832-a, p. 32) there is a perfectly accurate and full description of the advehent and revehent veins of the mesonephros, the great anastomosis between the revehent veins, and the union of the right one with that part of vena cava which traverses the liver. On this same page there is a description of the conditions in an embryo adder so young (according to Rathke's description) that no connection had yet been formed between the right revehent mesonephric vein (early right *subcardinal* of Lewis) and the hepatic circulation, although advehent and revehent mesonephric veins were said to be well developed. This is Rathke at his best.

On page 40 (1832-a) Rathke describes the dextral revehent mesonephric vein of the lizard embryo, and states that it

hatganz dieselbe Lage wie bei Schlangen, nimmt aus der untern (i.e., ventral) Seite der falschen Nieren eine grosse Menge von Venenzweigen auf, und senkt sich mit ihrem Stamme in einiger *Entfernungen der Gekrösvene* auf, und rechts von dieser in die Leber, wo sie dann als hinten Hohlvene erscheint.

His description of the revehent mesonephric veins of the snake embryo (1832-a, p. 32) contains this statement: "Beide Venae renales revehentes verbinden sich endlich dicht vor der falschen Niere der rechten Seite einem sehr spitzen Winkel zur Vena cava."

Rathke's description of the Vena renalis advehens of the Boa Constrictor embryo (1832-a, p. 32) is clearly reminiscent of his earlier (1830-a) description of the mesonephric segment of his mammalian "hintere Hohlvene" (posterior cardinal vein of present terminology). He stated that in the snake embryo the advehent mesonephric vein "lauft nach vorne und oben hinauf, legt sich an die äussere Seite der falschen Niere, und zwar ganz nahe am obern Rande derselben . . . ." Of his "hintere Hohlvene" in the mammalian embryo he had stated (1830-a, p. 64): "Auf einem jeden dieser genannten Organe (der falschen Nieren) und zwar auf der äusseren Seite ganz in der Nähe der oberen Rande derselben dicht über dem Eier und Samenleiter, verlief von hinten nach vorn eine Vene . . . ." The latter vessel is shown in Rathke's Tafel 1, Figure 1 (1830). This figure is reproduced as his *Tab.* 4, figure 1, (1832-b) and it is copied as figure 24 of the present account. It seems unreasonable and unjust to infer that Rathke was unaware that a part of

the V. cava traverses the liver, or that the work of Stark supplied him with his first information to that effect. When he described his "hintere Hohlvene" as migrating from the dorso-lateral border of the mesonephros "gegen die Aorta hin," he can scarcely be accused of supposing that an intra-hepatic vessel could ever lie against the aorta. He used the too-inclusive term "hintere Hohlvene" at times to designate part of the vessel, such as the postrenal part or that part in the caval mesentery. This is insufficient reason for supposing that he knew nothing of the hepatic part of V. cava or its development. More recent writers who have criticized him on this point have actually called revehent mesonephric veins "V. cava inferior." Again, in 1832, so far as the mammal is concerned, Rathke made no effort to describe the development of the hepatic part of V. cava. He had some knowledge of the development and function of the structure which, after Hochstetter, we call "caval mesentery." This he described developmentally (1832-b, p. 49) as "eine beträchtliche Ablagerung von dichtem Schleimstoffe," which (he states) serves as a passage for the V. cava. He is of the opinion that in 1806 Oken first correctly interpreted it in the dog embryo (Oken und Keiser's Beiträge zur vergl. Anat., Heft 2) and called it "die markige Brücke." Rathke calls it "die Okenschen Brücke." Hochstetter (1893, p. 564) awards credit for the original discovery of the structure to Goette (1875) in preference to Goette's successors: Lockwood, His, Ravn. I offer this detail as further evidence that Rathke knew that V. cava traverses the liver. The existence of the hepatic part of human V. cava inferior had been commonplace knowledge for several centuries. Cuvier, J. F. Meckel (1831, *Th.* 5), and numerous predecessors as well as contemporaries of Rathke were aware of it in mammals other than man. Meckel (1831) classified vertebrates upon the manner in which the venous blood from the caudal part of the dorsal body wall reaches the heart. He placed the dipnoi, amphibia, and what we now call amniota in a group in which this drainage traverses the liver. Von Baer gave evidence of his mastery of the subject of hepatic vena cava from its developmental side, before Stark expressed himself upon that subject. Rathke (1833) gave a very complete discourse upon the relation of omphalomesenteric veins to yolk sac and liver. For a somewhat different estimate of Rathke and Stark, consult the accounts of Kerschner (1888-a, p. 812), Hochstetter (1893, p. 611), and Butler (1927, p. 269). I shall quote only Hochstetter, who states:

> Stark ist der Erste, welcher angiebt, dass das Endstück der V. omphalo-mesenterica später zum Endstück der V. cava inferior werde und das die Strecke der Hohlvene zwischen Leber und Nieren mit dem Auftreten dieser Organe zur Entwicklung komme.

Rathke's account of the V. cava in mammals in 1832 (b), incidental to an account of the genital system, is essentially a reiteration of his statements in 1830, with certain details added. Here (*loc. cit.*, p. 82) he definitely describes his "hintere Hohlvene" as "dissociating itself" from the right "falsche Niere" and taking up a position lateral to and close to the aorta. He states that his description applies almost entirely to the pig. He describes the disappearance of almost all the transverse veins on the dorsal side of the mesonephros, and their functional replacement by one large transverse stem. He gives a clear description of the veins upon the medial surface of the mesonephros and gives their history probably more adequately than any subsequent author has done. He gives a clear description of the origin of the renal

drainage into the cross-anastomosis between the medial veins of the mesonephros. He describes vessels for the earlier and the later drainage (consult my figures 26 and 27) of the gonad of the ungulates. He states that with the descent of mesonephros and gonad, the original caudal mesonephric tributaries to the ungulate postrenal vena cava enlarge to produce sex veins entering the latter vessel just cranial to the Vv. iliacae. This he would seem to have regarded as a peculiarity of the ungulate embryo. (Consult Butler (1927) and Reagan and Tribe (1928-b, p. 492).)

### THE WORK OF VON BAER

We may now consider the work of von Baer, then the work of Stark, after which we may return to the final view of Rathke. In 1828 (*Entw. der Thiere, Th.* I, p. 71) von Baer described clearly, under a terminology of his own, those vessels which we now call Vv. cardinales anterior and posterior, and ductus Cuvieri. His description applies to the five-day chick embryo (figures 17, 18 and 19). He described on each side a "Drosselvene" which drains caudally to meet a posteriorly located, cranially coursing vessel. This vessel is described thus: "Im untern Rand jeder Bauchplatte ist eine Vene, die mit der Drosselvene jeder Seit vor dem Eintritt in das Herz sich verbindet." This hinder vein is designated as an "Intercostalvene." In a footnote on page 136 of the second part of his *Entwickelungsgeschichte* he stated that his preceding term was the result of a typographical error; that he had meant the vessel to be called "Subcostalvene." On page 71 (1828), in addition to vessels clearly recognizable as Vv. cardinales posteriores of present terminology, he described on each side ventro-medial "Gefässstämme, auf denen die Wolffschen Körper sich

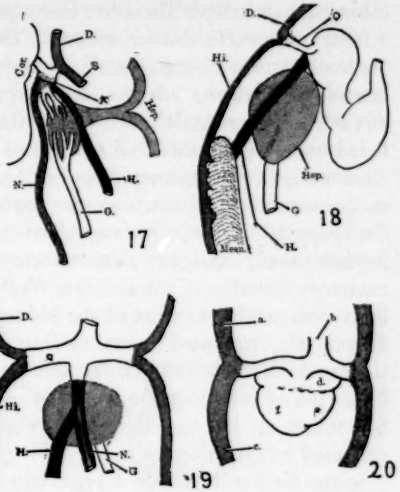



FIG. 17. ENLARGED DETAIL FROM A DIAGRAMMATIC SAGITTAL SECTION OF A FIVE-DAY CHICK EMBRYO

(Simplified from von Baer's *Tafel* 2, figure 8, 1828.) *G*, "Gekrösvene" entering the liver (Hep.); *H*, that part of V. cava within (what is now termed) the caval mesentery; *Hi*, "hintere Hohlvene"; *K*, "Körpervenenstamm"; *Vv.h.*, hepatic veins; *N*, "Nabelvene"; *Cor.*, heart; *D*, "Drosselvene" (equivalent of V. cardinalis anterior); *S*, "Subcostalvene" (equivalent of V. cardinalis posterior). In the original figure, no attempt was made to show through the liver as a transparent object that part of V. cava passing within the right lobe of it. The "Gekrösvene" was shown in orange color. The other veins were shown in blue.

FIG. 18. ENLARGED DETAIL FROM VON BAER'S TAFEL 4, FIGURE 17 (1837)

The portion of von Baer's manuscript describing several of his illustrations was published only posthumously and edited by L. Stieda, who states that the manuscript contains no detailed explanation of the figure. According to von Baer's general description, the structures may be believed to be as follows: *D*, "vordere Wirbelvene" (equivalent of V. cardinalis anterior); *H*, "Hohlvene"; *Hi*, "hintere Wirbelvene"; *G*, "Dottersacvene"; *Hep.*, liver; *Q*, "der venose Querstamm." The figure probably represents a five-day chick in left-lateral view.

FIG. 19. ENLARGED DETAIL FROM VON BAER'S TAFEL 4, FIGURE 10 (1837), SHOWING IN VENTRAL VIEW THE VEINS NEAR THE HEART OF AN AVIAN EMBRYO

(Abbreviations as in the previous figure; in both copies the legends are changed for the sake of uniformity.) *N*, "Nabelvene."

FIG. 20. DORSAL VIEW OF THE HEART AND RELATED VEINS OF A "YOUNG" SHEEP EMBRYO

(After Rathke, 1830-a, *Tafel* 1, figure 1.) *a*, "vordere Hohlvene"; *b*, "Lebervene (nach vorn umgeschlagen)"; *c*, "hintere Hohlvene"; *d*, atrium; *e* and *f*, indications of the ventricles.

bilden . . . . und also die Hauptwurzeln der untern Hohlvenen wären." These "roots of the vena cava" (revehent mesonephric veins) are the caudal parts of early "subcardinals" of recent authors. It is interesting to note that authors of the time thought the mesonephros of amniotes to be a product of the vascular system. On page 98 (1828) he suggested that further study might demonstrate an excretory function of the amniote Wolffian body comparable to that of the kidney of fishes. He attempted (p. 97) to determine the nature of the Wolffian body and vessels by means of injecting the revehent veins, but found all the mesonephric structures obscured by the injection.

Space does not permit a reiteration of all the statements of von Baer which prove that he had a knowledge of the hepatic part of the V. cava. My figures 17, 18, and 19 contain parts of von Baer's Tab. 3, figure 2 (1828). On p. 59 (*ibid.*) he describes accurately the formation of the liver in relation to the omphalomesenteric veins. On page 93 he describes the course of the "Nabelvene" in the liver and states that it

> verbindet sich . . . . dann am vordern Ende dieses Organs mit einer Lebervene, die sich sogleich in die Hohlvene, deren Stamm von oben sich in die Leber eindrückt, einmündet. Mann kann also fast mit demselben Recht sagen, dass die Nabelvene in den Stamm der Hohlvene geht, oder dass sie in eine Lebervene sich mündet. Der Theil der Nabelvene, welcher nach der Vertheilung in die Leber bis zum Hohlvenensystem reicht, wäre dem ductus venosus Arantii der Säugethiere zu vergleichen.

The relation of his "stem" of the V. cava to the Wolffian body is discussed on his page 81 (1828, *Th.* 1): "Am 5ten Tage sieht man deutlich den Stamm der Hohlvene mit vielen kleinen Wurzeln aus der innern Seite der vordern Enden beiden Wolffischen Körper hervortreten und hinter der Leber hinaufsteigen." Again on page 98, concerning the chick,

> dass vom fünften Tage an deutlich aus dem vordern Ende des Wolffischen Körpers eine starke Vene hervortritt, die mit, oder vielmehr jetzt den Stamm der hintern Hohlvene eben so ausmacht, wie in später Zeit die beiden Hauptwurzeln der hintern Hohlvene . . . hervortreten.

From a posthumous supplement to *Theil II* of von Baer's *Entwickelungsgeschichte* (the supplement was edited by L. Stieda, in 1888) we find that the Manuscript for *Theil II* was finished in 1834. On page 136 of this account (Theil 2) the following occurs:

> Diese hintere Hohlvene ist noch . . . . sehr kurz. Man sieht dann aus der innern Fläche des vordern Endes jeder Primordial-Niere einen Blutstrom hervortreten. Beiden laufen zusammen in ein Stämmchen, das, wie der Erfolg lehrt, die hintere Hohlvene wird. . . . . sie geht an der obern Wand der Leber vorbei und wird hier ein Zweig des allgemeinen Venenstämmes.

Unfortunately it is impossible to discuss fully the beautiful work of von Baer (1834) upon the porpoise. He describes a "double" postrenal V. cava, the absence of azygos veins, and especially the primitive, plexiform (*geflechtartig*) condition of the venous system. For the information of those who prefer to believe that our fundamental concepts of the vascular system have been arrived at only recently by a fortunate few, this passage from von Baer's (1834) page 10 (402) is offered:

> "Überhaupt scheint mir auch darin die Familie der Cetaceen den niedern Wirbelthieren sich zu nähern, dass das Venensystem viel weniger dem Arteriensystem gleich bildet ist, als in den übrigen Säugethieren.
>
> Die frühzeitige Auflösung der Venenstämme in Geflechte, oder richtiger gesprochen, indem wir von der Peripherie nach dem Centrum vorschreiten, das späte Sammeln der Venengeflechte in Stämme, wodurch die Cetaceen sich vor andern Thieren auszeichen, scheint für die Vergleichende Anatomie von grosser Wichtigkeit. Bedenkt man nämlich, dass in Embryonen Zustande auch die grossern Gefäss-Stämme, und namentlich die Venen, geflechtartig auftreten, dass, um nur *ein* bekanntes Beispiel

hervorzuheben, in Fisch-Embryonen selbst die Aorta durch ein weites Geflecht in den Stamm der hintern Hohlvene übergeht, wie Döllinger so schön dargestellt hat, so zeigen die Cetaceen herein nicht nur eine gewisse allgemeine Embryonen-Aehnlichkeit, sondern man kann auch, wenn man weiter sieht, erkennen, wodurch diese allgemeine Embryonen-Aehnlichkeit selbst hervorgebracht wird."

Von Baer then states that John Hunter (1787) saw and noted conditions of this sort in the whale. On page 332 of Hunter's account there is reference to the sluggish manner of circulation in the whale, and to the tendency of the vascular system here to maintain a widespread net-like condition, which Hunter described as reminding him of the pampiniform plexus of the bull. Consulting Allen Thomson (1832), we find that Hunter correlated the retention of embryonic plexuses in the adult sloth with the sluggishness of habits and of circulation in these creatures. Spallanzani (1801) noted that in regenerating tails of urodeles the first vessels are capillary plexuses similar to those of early embryonic development; that the great caudal vessels are regenerated out of such plexuses.

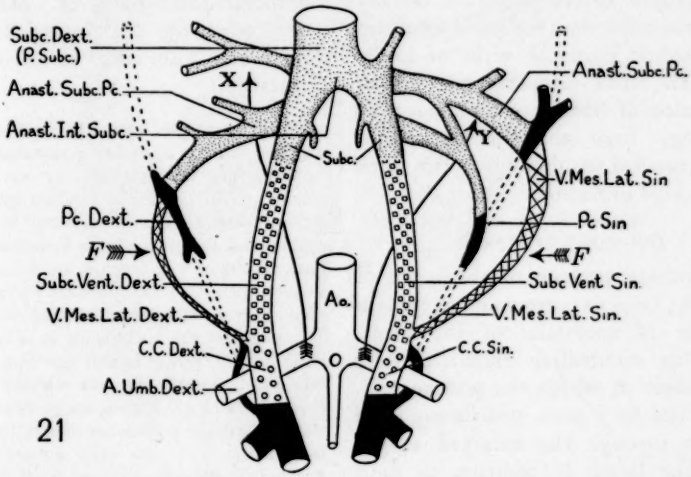



FIG. 21. RECONSTRUCTION OF A PORTION OF THE VENOUS SYSTEM OF A 14-MM. SHEEP EMBRYO

(Harvard Embryological Collection, Series 1106, after Butler, 1927, figure 9, p. 299.) *P.C., dext. et sin.*, degenerate remains of Vv. cardinales posteriores; *Subc.*, "subcardinal veins"; *Subc. Vent.*, "Ventral subcardinal veins." The figure is of interest in making intelligible the descriptions given by Stark (1835), and in rendering improbable the supposition that Rathke ever saw "cardinal veins" (posterior cardinals) and the anlage of postrenal V. cava present in any given specimen of sheep embryo. Postrenal V. cava has not yet appeared.

In 1835, von Baer published his beautiful and accurate work upon the development of the teleost fish. Here he abandons the terms "Drosselvene" and "Subcostalvene." For them he substitutes the terms "vordere Vertebralvene" and "hintere Vertebralvene." The common stem which unites the two veins is called "truncus transversus" (consult my figure 23). It should be noted at once that these vessels are comparable to our present badly named anterior cardinal, posterior cardinal, and the duct of Cuvier in fishes. They are not to be confused with the "vertebral veins" of Rathke (1838).

In 1835, von Baer objected to the use of the term "hintere Hohlvene" as Rathke had employed it. On page 25 (*ibid.*) he states:

> Diese *hintere Vertebralvenen* sind allerdings wohl dasselbe, was man in Fischen gewöhnlich die Hohlvene (denn man spricht gewöhnlich nur von Einen) zu nennen pflegt, aber wohl mit Unrecht, wenn man damit dasselbe Blutgefäss zu bezeichen glaubt, das in Säugethiere diesen Namen führt.

Then in a footnote he states that for the teleost fish the hepatic (omphalo-mesenteric) circulation contains the only venous structure to which the term V. cava is applicable. Von Baer's term "posterior Vertebral vein" fared no better in the evolution of our terminology than did his term "Subcostal vein." Yet these terms represent a reaction against the misnomer "V. cava inferior" as it had been employed to designate the earliest veins in the embryonic bodies of amniotes and the adult posterior veins of lower fishes. His terms represent progress in the direction of liberating embryological terminology from the domination of adult anatomical terminology. His work was dedicated to Rathke.

### THE WORK OF STARK

The primary purpose of the work of Stark (1835) was to portray and to explain a number of anomalies of the veins. Among his mammalian anomalies were five instances in which the postrenal V. cava drained by a path, not through the liver but through the enlarged azygos veins. The latter, in addition to their normal function, had assumed that of draining the entire infrathoracic region, in the absence of the part of V. cava normally found in the caval mesentery. In adult amphibians, reptiles, birds, and mammals, Stark attacked the problem experimentally by ligating the V. cava at the level of the caval mesentery and injecting the veins at points caudal to the ligature. He studied the collateral venous lines by which the injecting-mass reached the cranial regions. He also injected mammalian embryos and foetuses. His chief interest was that of thoracic drainage. To the embryonic mammalian structures to which Rathke had (1830) so unfortunately applied the term "hintere Hohlvenen" Stark applied the equally unfortunate adult terms V. azygos and V. hemiazygos.

Rathke (1830-a), according to Stark, made two statements which Stark regarded as incorrect. The former said that the sheep has no (dextral) azygos veins; he said (according to Stark) that the hepatic vein enters the structure which we now call the right duct of Cuvier. I am unable to see that this implies that Rathke believed the cranial segment of (what we now call) posterior cardinal vein becomes incorporated into the liver. Stark (1835, p. 27) offers the criticism of Rathke, of which the following is an attempted translation:

> One of these veins (*hintere Hohlvenen*), the sinistral one, our eminent Authority maintained to be the V. hemiazygos, while the other one was the V. cava inferior. With the first part of his assertion I am entirely in agreement. It can not be reasonably doubted that the left one is the V. hemiazygos. But I can not concur with him that the dextral one is the V. cava inferior. I should for my part take it to be the V. azygos. He seeks to champion this opinion by observing that the V. hepatica is admitted to the trunk which is formed by this vein with the jugular vein, and that in the sheep the dextral *V. sine pari* is obviously lacking. Begging the pardon of a man for whom I have the profoundest respect, this statement is incorrect . . . . the other argument which he derives from the inosculation of the V. hepatica into the common trunk of the right hand side does not, I think, count for much, since the V. hepatica almost invariably enters the cavity of the atrium some distance from the V. cava superior, and, indeed, from the lower side. . . . .

Now the existence of a normal right azygos vein in human anatomy had been recognized since Vesalius (1543) published his *Fabrica*. The existence of a hepatic part of V. cava inferior was known even earlier. Whether Rathke (one of the greatest anatomists of his time), like a large number of contemporary comparative anatomists, (consult Meckel, 1831, *Th.* 5) positively knew that many mammals and man have functional dextral azygos veins, I should be reluctant to offer doubt. Granted that he was to this extent informed, it is preposterous to

suppose he believed such animals to be devoid of Vv. cavae inferiores; and it is equally absurd to suppose that he believed his right "hintere Hohlvene" to form both vessels in animals possessing both.

Stark (1835, *Tab.* 2. figure 8) gave an excellent figure of a young sheep embryo which had been injected and dissected by Prof. Huschke. The figure itself (consult my figure 25) was drawn by Prof.

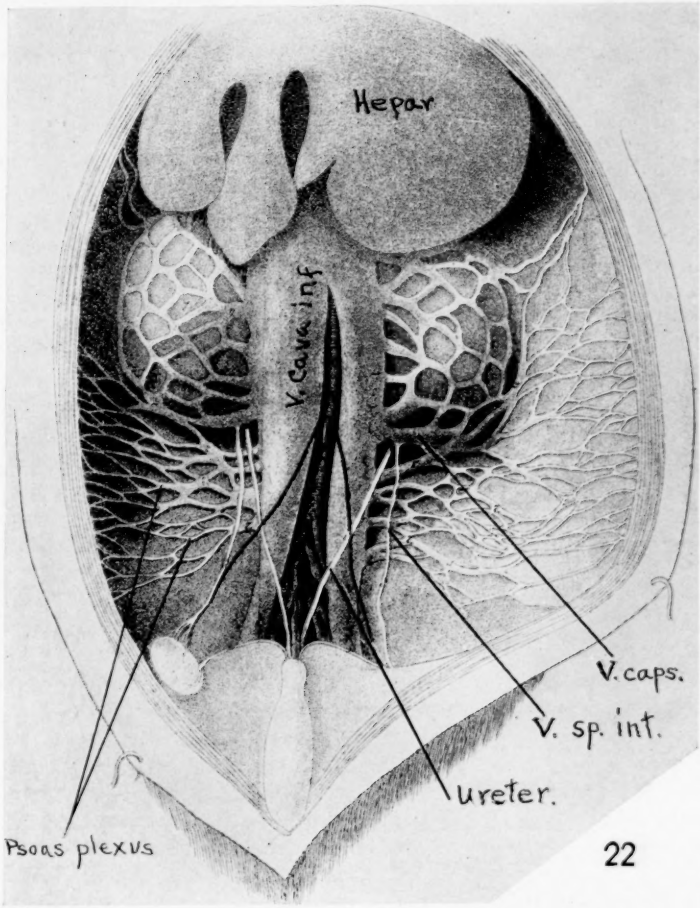
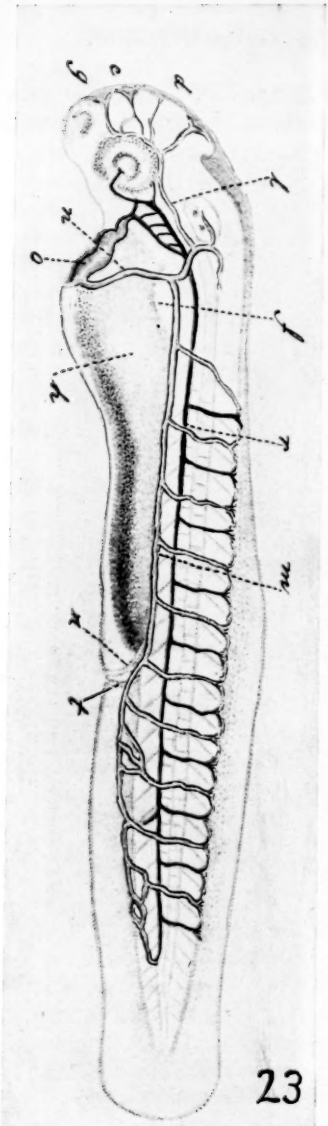



FIG. 22. VEINS OF DORSAL WALL OF ABDOMINAL REGION OF A SEAL

(From A. Burow, 1838, *Taf.* 7.) The figure shows a normally persistent left homologue of postrenal V. cava in addition to that structure; these are both called iliac veins in the original figure. The internal spermatic veins (*V. sp. int.*) drain into the drainage system of the renal capsule (*V. caps.*). The venous plexuses caudal to the kidneys were called "psoas plexuses." No attempt has been made to carry out the original labelling of the figure. It is hoped that the figure may be of interest in connection with work which greatly needs to be done on the nature and development of the vascularization of the renal capsule. Subperitoneal plexuses continuous with embryonic "psoas plexuses" are reflected around ventrad of the peritoneal cavity. From this general plexiform system are derived the veins of the renal capsule, the ureter, and certain veins of the ventral body wall.



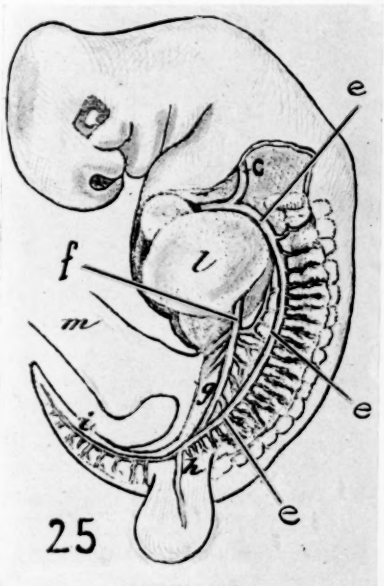


FIG. 23. THE VASCULAR SYSTEM OF AN EMBRYONIC TELEOST FISH CYPRINUS

(From photographic enlargement of von Baer's figure 20, 1835.) *f*, anterior extremity; *g*, nasal pit; *h*, yolk sac; *l*, "vordere Vertebralvene"; *m*, "hintere Vertebralvene"; *n*, "Querstamm (truncus transversus)"; *o*, atrium; *r*, aorta dorsalis; *t*, "harnleiter." Note especially the beautifully illustrated intersegmental vessels.

FIG. 24. LATERAL VIEW OF A "VERY YOUNG" SHEEP EMBRYO

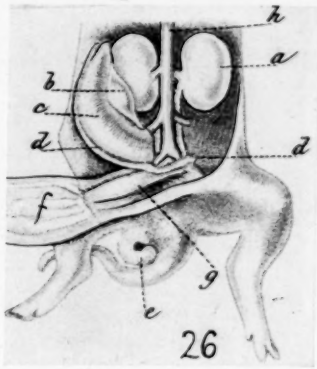
(After Rathke, 1830-a, *Tafel* 1, figure 1.) *a*, left atrium; *b*, ventricle; *c*, liver; *d*, "Luftröhre;" *e*, alimentary tract; *f*, "mesonephros and its efferent duct and the *hintere Hohlvene*"; *g*, "funnel of the allantois"; *hh*, the "two Nabelvenen."

FIG. 25. LEFT SIDE OF A "YOUNG" SHEEP EMBRYO

(After Stark, 1835, *Tab.* 2, figure 8, photographically enlarged.) This remarkable figure was executed by Prof. Huschke from an embryo which he had injected and dissected. *c*, truncus venae cavae superius; *d*, vena jugularis; *eee*, "V. azyga sinistra"; *f*, "Vena cava inferior"; *g*, "pars ejusdem inferior conjunctionem cum V. sine pari contrahens"; *h*, V. cruralis; *i*, V. caudalis; *l*, hepar; *m*, funiculus umbilicalis.

Huschke. The embryo is described as having no nose, no eyelids, an incompleted iris, and palp-like limbs. The posterior cardinal (labelled *V. azyga sinistra*) vein which can be seen exhibits no tendency towards degeneration. In the embryos of ordinary eutherian mammals (rodents included) having a non-marsupial type of postrenal V. cava, the anlage of the latter vessel is usually not present so long as the posterior cardinal vessel is so strongly functional as the "V. azyga sinistra" of this figure is shown to be. A vessel (*f*) draining into the liver is called V. cava inferior. This, in turn, drains a vessel (*g*) described as anastomosing caudally and laterally with the "V. azyga sinistra" (*e*) and with the "V. cruralis" (*b*). Throughout its course, the vessel labelled *g* receives mesonephric tributaries described as "V. fine pari contrahens." Stark (p. 29) mentions that "again, in another sheep embryo a little older, Prof. Huschke, who made an injection of the V. cava inferior and thereby filled the V. azygos, distinctly saw the V. cruralis uniting with it." Stark emphasized the fact that in these two sheep embryos only was it possible to obtain conditions such as those shown in his figure just described. His study also comprised relatively older embryos of the sheep, the cow, and man. In the latter he experienced difficulties with injection. He mentioned even larger vessels than his his vessel *g* on the ventromedial surfaces of Wolffian bodies in later stages, but found it impossible to inject the "crural" veins from them; with increasing age, such vessels were found to become even shorter. Concerning his vessel *g* and the general conditions in his *Tab.* 2, figure 8 (see my figure 25) he states (p. 29):

As, however, we have been able to observe this arrangement of the veins in only one or two cases, I should like to have it confirmed by further experiments on the part of other observers (Cum vero semel iterumque tantum hanc vasorum rationem deprehendere nobis licuit, ab aliis quoque observatoribus eam pluribus experimentis confirmatam velim).



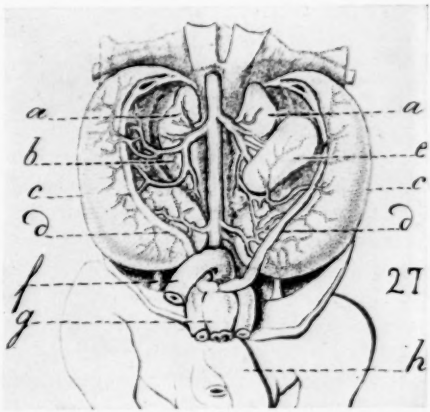




FIG. 26. DISSECTION OF THE HINDER PART OF A SHEEP EMBRYO WITH BODY WALL, ALIMENTARY VISCERA, AND THE LEFT MESONEPHROS AND GONAD REMOVED

(After Rathke, 1832-b, *Tafel* 3, figure 9.) *a*, metanephros; *b*, gonad; *c*, "Eierleiter oder Samenleiter"; *e*, external genitalia; *f*, umbilical cord; *g*, urinary bladder; *h*, "hintere Hohlvene."

FIG. 27. DISSECTION OF THE HINDER PART OF A PIG FOETUS

(After Rathke, 1832-b, *Tafel* 4, figure 3.) Most of the viscera and the right gonad were removed. *a*, suprarenal gland; *b*, metanephros; *c*, mesonephros; *d*, "Eier- oder Samenleiter"; *f*, hind gut; *g*, urinary bladder; *h*, external genitalia. Note especially the veins taking care of the caudal drainage of the mesonephros.

From Kerschner (1888-a) one gets the impression that Stark actually saw in the figure described the true anlage of postrenal V. cava. The fact that Stark failed to find his vessel *g* in older stages of embryos of different species has been noted. On page 35, in Stark's final summary is this statement:

> As to the part of the V. cava which remains to be perfected between the kidneys and the iliac veins, I was not privileged to see how its nature is changed during development. Until the eyes of man have been able to discern this process, conjecture must be accepted (Quae denique Venae cavae inferioris perficienda restat pars inter renes et vasa iliaca sita, quomodo in ea fabricanda natura versetur, deprehendere nondum concessum fuit. Quod naturae opus priusquam fortuna cuipiam mortalium oculis conspiciendum obtulerit, conjecturae concedendus erit locus).

From what has been quoted, it would seem that Stark did not regard his vessel *g* as the anlage of postrenal V. cava. It is probable that he was dealing with a condition peculiar to the sheep, such as that found by Butler (1927) temporarily to exist in the sheep embryo (consult my figure 21, reproduced from Butler's figure 9). In this figure of Butler's, the posterior cardinal vessels have degenerated far more than they have in the figure from Stark, yet in the figure from Butler, the principal anlage of postrenal V. cava has not appeared. In the later stages of Butler's highly interesting series of sheep embryos the large vessels ventral or medial to the mesonephros have disappeared, and the draining of the caudal region has been assumed by anlagen of postrenal Vv. cavae. Hochstetter had noted (1893) that the arrangement of veins in connection with the mesonephros of the sheep is atypical.

On pages 27–28, Stark (1835) further criticises Rathke:

> But ponder carefully the remarkable and very obscure transition in the course of which, according to Rathke, the right vein (*hintere Hohlvene*) is changed into the V. cava inferior in such a manner that one half, the upper half of this self-same vein, is disengaged from the spurious kidney and carried above its dorsal edge towards the aorta and between the Wolffian bodies, while the other, the posterior part, remains stationary on the upper edge of the spurious kidney. We need not fear that we shall diminish the credit of this farsighted Scholar, or injure his reputation, if we suspect that, in a matter so highly complex and where no one has had the opportunity of observing the series of changes from beginning to end, the V. cava inferior, which decreases in size from the liver caudally towards the kidneys and which goes to meet the veins which come from them, was thought by him to be the V. azygos, which gradually comes to naught in the region of the kidneys.

In Rathke's account I find no occasion for the inference of Stark that Rathke mistook the region of V. cava between liver and kidney to be a degenerating V. azygos. Consultation of Rathke's figures will afford conclusive evidence (see my figures 26 and 27; see also p. 194) that Stark was misinformed when he represented Rathke as claiming that the postrenal portion of his "hintere Hohlvene" remains stationary on the lateral side of the Wolffian body. The principal point of interest is this: Stark exhibited a healthy skepticism of "the obscure process of transition" by which a vein lying dorsolateral in the mesonephros extricates itself from that organ and comes to lie close to the aorta. In most eutherian mammals in which postrenal V. cava does not conform to the monotreme-marsupial type (for the latter type consult Hochstetter, 1893, *Tafel* 23, figures 27 and 28; 1896, *Tafel* 18; McClure, 1900; 1906-b; Tilney, 1912; Tribe, 1923) we have gradually come to recognize that the greater part of postrenal V. cava ordinarily arises from a circulation collateral to the posterior cardinal. In most cases these vessels coexist temporarily, separated from each other by the kidney. There remain certain mammals (the guinea

pig and the rat) in which it is claimed that postrenal V. cava in its entirety is a remains of the original posterior cardinal line. This implies either that the posterior cardinal frees itself from intimate association with the Wolffian body, or (Butler, 1927, p. 330) that this association, which has never been very intimate (*ibid.*, figure 20-M), becomes even less so (*ibid.*, figure 22–O) as the permanent kidney effects a separation.

Views essentially similar to this have been held by Zumstein (1897) and by Begg (1917). The kidney is described as growing ventral and lateral to the posterior cardinal (consult Hochstetter, 1902, p. 143). From a certain amount of study of injected rat embryos I am convinced that the kidney of this animal remains medial to the main part of the lumbar posterior cardinal; that the latter vessel remains intimately associated with the Wolffian body and degenerates very rapidly as a collateral circulation is established medial to the kidney; that the vessels labelled *Pc.* in Butler's figure 22–O (1927) are not posterior cardinal veins, but rather that they are new vessels comparable to those described as "lumbar supracardinals" by the users of the latter term; that the postrenal posterior cardinal has degenerated partly or completely at the site of its original position in the mesonephros; that the correlation of mesonephric function and posterior cardinal persistence is not necessarily a negative one; that the indefinite enlargement of any or all elements of the "supracardinal plexus" of Butler's figure 21-N would fail to produce a vessel comparable to postrenal V. cava of any known mammal; that Stark's criticism of Rathke on the "obscure process of dissociation" of cardinal vein from mesonephros is applicable here. Future conflict of opinion upon the subject is most likely to be carried on between those observers who think that the history of V. cava can be worked out from reconstruction of a few stages of development, and those who believe it can not.

Stark and Kerschner had much in common. Each was fascinated by anomalous veins, and each sought to explain them largely by what he could find in the literature of his time. Each brought to light much valuable historical material. Neither did a great deal of embryological investigation. In the writings of either of these authors, one feels that here was a prelude to something tremendous which failed to materialize. On page 35, Stark makes this statement: "From the crural veins two new veins branch on either side towards the interior; these unite at the fifth lumbar vertebra to form a common trunk and constitute the newest part of the ascending V. cava, the part below the kidneys." He does not mention the source or age of any material studied in support of this statement. Kerschner derives postrenal V. cava from an "attenuated iliac vein."

The last statement ever made by Rathke upon mammalian veins occurs in the final sentence of the final chapter in his posthumous work in 1861. Here it is stated that the cranial-most segment of V. cava inferior is intrahepatic, and is derived from the omphalomesenteric vein. Stark had stated (1835, p. 27): "With his leave, I should be persuaded to think that our celebrated Authority took to be V. hepatica that which was V. azygos accessoria." (Consult my figure 20.)

### THE HEPATIC CIRCULATION

From Rathke's account (1830-b) of the formation of the hepatic portal and the revehent hepatic veins, it is clear that he had made no pretence of following the history of those veins in his earlier work (1830-a). In his article (1830-b) devoted specifically to the hepatic circulation there is described (p. 437) a *Nabelvene*, the posthepatic portion of which in later stages is joined by a *Gekrösvene* to form the *Pfortader*. The vitelline and mesenteric veins are evidently described as forming the hepatic portal vein. The *Nabelvene* is described in early stages (p. 435) as having an uninterrupted course through the liver. It is said to join the transverse stem (duct of Cuvier of present usage) formed by the union of the

"vordere und hintere Hohlvenen." That part of the *Nabelvene* joining the transverse stem is called V. hepatica (see my figure 20). On p. 436 (*ibid.*) he states that the middle part of the intrahepatic portion of the *Nabelvene* becomes constricted, so that its cranial part becomes revehent and its caudal part becomes advehent to the liver. He states that the cranial remnant is "die wahre V. hepatica" while the caudal remnant helps to form hepatic portal vein. He then describes anastomoses between the hepatic circulation and the right and left "halves of the *hintere Hohlvene*." These are said to take place at the level of the cranial face of the liver. These anastomoses are said to form a new common stem which enters the V. cava. The cranial remnant of the *Nabelvene* is then said to degenerate. Thus a new hepatic vein is said to form. The description is very obscure. On page 436 he evidently describes the early formation of that part of V. cava lying in the caval mesentery: "zwei bis drei andere kleinere Gefässe, dagegen treten aus dem hintern Theile der rechten Hälfte der Leber hervor und münden sich in einer Reihe hinter einander in die Hohlvene ein." It is still possible to believe that Rathke's principal difficulty was one of terminology. If we are justified in believing that Rathke regarded the right posterior cardinal (of present usage) as transforming into V. cava in the cranial thoracic region, we may equally well accuse Stark of having believed that the entire lumbar region of that same vessel forms azygos vein.

There is reason to believe that Stark was not aware of Rathke's work (1830-b) on hepatic circulation. In the descriptions at that time no provision was made for a separate embryonic cardiac chamber, the sinus venosus. In the light of this fact, Rathke's description of hepatic part of V. cava as entering the common trunk of (what we now call) right anterior and posterior cardinal veins is a less serious error than Stark supposed.

The published record of the celebrated seminar given by Rathke (1838) is unillustrated. It is largely a mass of generalization often without specific mention of materials observed or sources of evidence. He described postrenal V. cava as taking its origin from the dorsal side of the venous stem connecting the hepatic part of V. cava with the renal anastomosis, and coursing caudally to the iliac region. He describes it as an unpaired structure. He does not state that it grows down from the liver. On this point, certain reviewers have misunderstood him. He states (p. 15) that the portion of V. cava behind the liver is formed in mammals "in ähnlicher Weise, wie bei den Vögeln." On pages 15–16 (concerning mammals) he states:

Die erste Andeutung der Hohlvenen fand ich bei Schafembryonen, die 6½ Linien lang waren. Zuerst entsteht der Stamm, dann ein Paar Aeste, von denen ein jeder in dem innern Rande eines Wolffschen Körpers eine geraume Strecke nach hinten entlang lauft, und viele Zweige von diesem Organe, einen Zweig aber auch ganz vorne von der Niere empfangt. Darauf wachst der Stamm über seinen Theilungswinkel noch hinaus immer weiter fort, indem er nämlich einen unpaaren in der Okenschen Brücke nach hinten laufenden Ast absendet. Dieser schickt nahe dem hintern Ende der Wolffschen Körper, zwischen denen er liegt, an dieselben ein Paar Seitenäste ab, von denen von jeder ausserdem einen Zweig an den Hoden oder Eierstock seiner Seite abgiebt. Hinter diesen letztern Aesten aber bildet sich zwischen dem Ende jenes unpaaren Gefässes und demjenigen Theile einer jeden V. cardinalis, in welchen die V. cruralis und V. hypogastrica derselben Seitenhälfte übergehen, eine kurze Anastomose, die an der obern Seite des Wolffschen Körpers hinter der Niere ihre Lage hat. Wenn nun die Cardinalvenen und die Wolffschen Körper vergehen, wird diese Anastomose zur V. iliaca, das vor ihr liegende oder hintere Paar von Seitenästen der Hohlvene zu den V. renalibus.

Sabin and Butler have conclusively shown that in the ungulate mesonephros there develop ventro-medial venous paths collateral to V. cardinalis posterior which functionally replace the latter prior to the establishment of the anlage of postrenal V. cava. Since Rathke's study was made

upon the sheep embryo, we may reasonably doubt whether he saw a "Veneninsel" similar to that seen by Hochstetter. It need scarcely be stated that he saw postrenal V. cava and V. hypogastrica coexistent.

In Rathke's account in 1838, he applies the term "Nabelvene" only to the umbilical vein and the term "Nabelgekrösvene" to the omphalomesenteric vein. His recognition of the adult derivatives of the allantoic and lateral line veins, and his interpretation of them in terms of the superficial abdominal veins in amphibians and reptiles are most instructive. He recounted these and several other phenomena for whose discovery Goette is usually given credit.

### RATHKE'S TERMINOLOGY

Rathke's great contribution in 1838 was that of improved terminology. His *vordere Hohlvene* (1830) was changed by him (1838) to *V. jugularis*. His *hintere Hohlvene* became *V. cardinalis* The common stem of these two vessels (*Sinus veineux* of Cuvier, 1805; *truncus transversus* of von Baer, 1835) became *ductus Cuvieri*. To earlier embryologists it had been a source of pleasure to imagine that they beheld adult structures in early embryonic stages. The commendable practice of using strictly embryological terms for strictly embryonic structures was indulged in with caution. Yet here was a serviceable, non-committal term *cardinal* involving, we may believe, the concept *principal*. Until so recently as the writing of Kölliker's *Grundriss* (see my figure 1), Foster and Balfour's *Elements*, etc., the terminology of Rathke was that ordinarily employed. Then some one conceived the idea of calling Rathke's *V. jugularis* by the name *V. cardinalis anterior* ("anterior cardinal," "precardinal," etc.); also the *V. cardinalis* of Rathke became the *V. cardinalis posterior* (posterior cardinal, "postcardinal," etc.). There are now several varieties of *subcardinals* and *supracardinals*. Ductus Cuvieri is sometimes called *common cardinal*. Sabin (1917) uses the latter term most inappropriately in an account of the early posterior cardinal vessel. We have no objection, for instance, to the military titles: "major general" and "adjutant general." The title "corporal general" would neutralize the forces of the words involved.

Space does not permit of a discussion of the articles by Rathke upon birds, crocodiles, turtles, etc.

* * *

In the present account, no attempt will be made to review the recent and well-known contributions to the subject. I need only mention the familiar work of Huntington and McClure (1907 and 1920), in which it is concluded that the (non-posterior-cardinal portion of) V. azygos and the postrenal V. cava are serially homologous, developmentally continuous structures, derived from a single, simple, continuous, longitudinal, dextral embryonic vein called the "right supracardinal vein." This is not the complete statement of their views, but it represents the fundamental concept of their theory. I have already taken the liberty to suggest (1927) that in the typical eutherian mammal the postrenal V. cava has a temporary cranial serial homologue (located largely in the caudal half of the thorax) which never enters into the formation of the azygos vein; that there exists in the lumbar region a caudal serial homologue of (the non-posterior-cardinal-portion of) typical V. azygos which takes no part in the formation of postrenal V. cava. The suggestion has also been made by Reagan and Tribe (1927–28) that the present descriptions of the veins ventro-medial to the mesonephros are

inadequate. It is not the purpose here to offer a review of the recent literature. This, however, may be said: whether we wish it or not, the formation of the V. cava is a much more complicated process than any existing account would indicate.

For the hospitality of the Department of Anatomy of University College, The University of London, I would express deepest appreciation. Access to the early nineteenth century collection which originally formed the libraries of Professor Sharpey and Professor Grant has been of great value, enabling me to secure for study a quantity of literature ordinarily unavailable. To Mr. F. Pittock, I am indebted for photographs of several original figures. Professor J. P. Hill and Dr. H. A. Harris have shown much interest in my efforts. Professors J. T. Wilson, G. Elliot Smith, and Arthur Robinson suggested many corrections of my original manuscript. The same is true of Dr. R. H. Hunter and Dr. R. J. Gladstone.

I regret that for the conservation of available space it has been necessary to indulge in very involved diction and an excess of parenthetical reference.

As one who is not a specialist upon the subject of V. cava, but merely as a reader interested in arriving at fundamental definitions of certain embryonic veins, I suppose I should apologize as a self-appointed reviewer of the subject. It was only after careful study of previous reviews that I felt justified in offering yet another. In no case have I meant to imply that independent rediscovery deserves less credit on point of originality than original discovery deserves. Doubtless there will be involved no unjustly unfavorable reflection upon the present era if we call to memory the work of those great masters of the science of Embryology, Heinrich Rathke and Karl Ernst von Baer. A knowledge of their remarkable achievements surely deserves to be perpetuated.

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# RESPIRATION IN THE INSECTS

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ONE of the major problems that had to be solved successfully in the course of the evolution of terrestrial forms of life was that of obtaining an adequate exchange of gases to support metabolism, and at the same time of avoiding the danger of desiccation. Most of the other essentials for terrestrial life had already been developed by many of the aquatic forms of the Cambrian period. These essentials included some means of locomotion, a skeletal framework supporting the organs of the body and serving for the attachment of muscles, and a circulatory system providing for the distribution of food materials and oxygen. At the same time these forms were generalized enough in structure to be adapted, with but slight modifications, to conditions of life on the land or in the air.

Respiratory mechanisms of various types and degrees of complexity had also been developed in these aquatic forms. In the smaller ones with no horny exoskeleton a simple exchange of gases between the blood and the water through the whole body surface sufficed. In larger forms and in those possessing thick or hard protective coverings, gills of various types were developed. The respiratory problem was comparatively simple even for those animals that left the water for the habitat of the beach or the swamp. Their respiratory mechanisms were but little modified from those of their aquatic ancestors and must have been of such a makeshift nature in the new conditions as to require the frequent return to the water or the presence of much moisture.

In the course of time, however, respiratory mechanisms were developed which enabled their possessors to become independent of the shore and marsh and to range far inland, occupying even arid and desert habitats. It is of interest to survey briefly the existing groups of animals that have developed successful mechanisms for bringing thin, moist membranes into contact with the air, and at the same time preventing an excessive loss of water. The list is surprisingly small. It includes a few species of Protozoa, the Mycetozoa; a few nematode worms; the earthworms and the land leeches among the Annelida; one small group, the snails and slugs, of the Mollusca; a few crustaceans, the Onychophora, myriapods, insects and arachnids of the Arthropoda; and four groups of the Chordata, the amphibians, reptiles, birds and mammals.

Furthermore, all of the groups in the above list except some of the arthropods and some of the vertebrates have, strictly speaking, solved the respiratory problem by evading it—that is, by living in extremely limited and essentially semi-aquatic habitats. The Mycetozoa live on wet, decaying leaves. The earthworms and the terrestrial nematodes live in moist earth or in decaying organic matter. Here, with no other respiratory organs than their thin, moist skins they are able to lead a lethargic life with a comparatively small energy expenditure. Even the

development of an efficient respiratory pigment in the blood and of an excellent circulatory system has not saved the earthworm from the limitations which its thin skin has placed upon it. The pulmonate molluscs seek shade and dampness, although they can exist in comparatively dry habitats. The pulmonary sac which they have developed would not seem to be very efficient, although they probably do not require a very considerable respiratory exchange for their slow lethargic movements. It could hardly be said that any of these groups had met the problem of air breathing with conspicuous success.

The arthropods and the vertebrates present a different story. Both of these phyla have produced forms which have succeeded in adapting themselves to terrestrial conditions of all sorts—the arthropods through at least three separate lines of descent, and the vertebrates through one. Even within these two groups, however, widely varying degrees of success have been attained.

All five of the classes of the arthropods have terrestrial or semi-terrestrial representatives. Two of these classes are entirely terrestrial or have secondarily aquatic species. A number of the crustacea have established a semi-terrestrial existence on the strand and shore, and a few tropical crabs even climb trees and go far inland. Their physiological mechanisms, however, are still essentially those of aquatic animals. They seek moist or damp habitats when ashore and return to the water to breed. Some of the isopods, the pill- and sow-bugs, do not return to the water to reproduce, but their habitats, under stones and wood, are very limited. The myriapods, with a primitive tracheal system similar to that of the lower insects, are still not a particularly successful group of air breathing organisms. All of the arachnids except the oldest, the Xiphosuria, are terrestrial. Some of the spiders have developed tracheae of the simple sort, but the book lungs of the rest are not greatly modified from the book gills of the ancestral forms. The arachnids were handicapped in their attempt to solve the respiratory problem by a late origin from aquatic forms that were already highly specialized. In spite of that handicap some of them are, at present, able to exist under arid conditions. They are, however, not given to very energetic lives, although they may be capable of considerable activity in emergencies. Of all the terrestrial arthropods, only the insects have developed flying forms.

Among the land vertebrates there is an interesting parallel between the efficiency of the respiratory mechanisms and the activity and the success of the group. The lung fishes, the amphibia and the reptiles are able to live upon land, and possess lungs which provide for gas exchanges without danger of desiccation. But the only mechanisms for ventilating the lungs are the swallowing of air and the enlargement of the thorax by the action of the intercostal muscles and the ribs. Such actions are not particularly effective, especially during activity. All of these forms are comparatively much less active than the most of the mammals. Even the reptiles are lethargic creatures. For food, they mostly await what may come their way, and for protection from enemies they rely much, as do many of the arachnids, upon defensive armaments, disagreeable secretions, poison glands and the like, rather than upon energy consuming activities. Physiologically, the rate of absorption of oxygen may well be the limiting factor in determining the level of activity an organism may show. It is, of course, possible for an animal in an emergency to go into debt for oxygen, but the amount of

such a debt is strictly limited, and the account must be settled promptly. In an organism which is able to meet only its ordinary demands, such a debt either could not be incurred, or would be repaid slowly with danger of collapse if another emergency should occur. It is quite possible that the large carnivorous reptiles of the late Mesozoic period were not as great a menace to the early mammals as they are commonly supposed to have been.

The mammals and the birds, on the other hand, have developed additional or accessory mechanisms for ventilating the lungs. The mammals have solved the problem successfully by dividing the ventral body cavity into two parts by the arched muscular diaphragm. The contraction of this muscle causes inspiration, and its passive return to the original position allows expiration. For the amount of energy expended, a much greater volume of air can be changed by such a mechanism than by the arching of the ribs by the intercostal muscles.

The birds have developed an extensive system of air sacs, in addition to their rather simple lungs. The bronchi communicate directly with nine large, thin-walled sacs, lying in the thorax and abdomen. At each inspiration nearly all of the air in the lungs is renewed, even when the bird is standing. During flight respiration is further assisted by the movements of the wings, and a still better ventilation is secured. The efficiency of the mechanism is indicated by the fact that the temperature of birds is usually higher than that of mammals, and also by the fact that flight, with a considerable energy expenditure, may be maintained for a long period of time. The flying insects show the same striking development of air sacs in the respiratory system as do the birds.

There are, then, only three groups of terrestrial animals that have developed highly successful respiratory mechanisms: the insects, birds and mammals. These three groups, furthermore, are energetic in their movements and are able to utilize continuously a large amount of energy in their muscular systems over a considerable period of time. The comparative activity and freedom of movement of all other terrestrial animals is slight. As for the insects, it is perhaps not an overstatement to affirm that, although other factors are undoubtedly involved, their signal success has been made possible by their adequately meeting the problem of providing a mechanism for gas exchange, sufficient not only for existence, but also for such energy consuming activities as rapid locomotion and flight.

### THE STRUCTURE OF THE RESPIRATORY SYSTEM

Malpighi, in his monograph on the anatomy of the silkworm, published by the Royal Society of London in 1669, was apparently the first to show that insects respire by means of anastomosing tubes, branching to all parts of the body and connected with the exterior. Aristotle, on the basis of observations that insects are very resistant to asphyxia, had placed them in a group of animals which he called non-breathers. Aristotle had, of course, no knowledge of the essential nature of the process of respiration, and considered that the air served only to cool the vital spirits in the lungs. The non-breathing animals, presumably, had vital spirits so poorly calorific that there was no necessity of any special mechanism for cooling them. Malpighi in his monograph devoted several plates to the tracheal system and also described it in a number of other forms than the silkworm. Since his time the detailed structure of the system and its modifications have been

described by many workers. Babak (1921) and Deegener (1913) have given excellent summaries of this and of the older physiological work, together with bibliographies.

The respiratory system in a typical perfect insect consists of a number of paired, segmental openings, the spiracles, and the tracheal tubes connected with them. The main tube leading from each spiracle soon divides into a number of large branches, some of which run longitudinally and unite with similar branches from the other main spiracular trunks. Other branches cross to the opposite side of the body and anastomose with the longitudinal trunks there. These main longitudinal and cross trunks give off a number of large branches, which in turn ramify everywhere inside of the exoskeleton, becoming smaller and smaller. Usually three large branches are given off in each segment from the main trunks; a dorsal branch to the dorsal muscles, a visceral branch to the alimentary canal and reproductive organs, and a ventral branch to the nerve ganglia and muscles. The head is especially well supplied by branches from the first spiracular trunk.

Every organ of the body is penetrated by a network of the smaller tracheal branches, which serve also the function of a connective tissue. True connective tissue is reduced to a minimum in the insects. The tracheae very largely take its place, anchoring the organs in place in the tube-like skeleton and holding together the elements composing the organs. The tracheoles are the terminal twigs of the respiratory tree. They are exceedingly slender tubes which arise from epithelial cells at the ends of the tracheal capillaries. They do not taper, have lumina less than one micron in diameter, and are unicellular in origin (Cajal, 1890; Holmgren, 1896). Anastomoses are common.

In structure the tracheae are homologous with the body wall. The same three layers are distinguished, the intima or chitinous cuticle, the hypodermis and the basement membrane. The intima, which is much thinner than the cuticle of the body wall, has one or more spiral thickenings, the taenidia, running the length of the tracheae. The taenidia extend to the tracheoles and play an important rôle in preventing the tubes from collapsing.

The Thysanura, considered the most primitive of the insects, show an interesting series of stages in the development of the respiratory system. One of the simplest forms, *Papirius*, has no tracheae at all (Lubbock, 1860). In another genus, *Machilis*, each spiracle supplies its own tracheal tree. There are no anastomoses of the branches from one spiracle with those from another (Lang, 1894). In other Thysanura, although the tracheal system is simple, both longitudinal and transverse anastomoses are present.

The spiracles, or stigmata, are arranged segmentally on the sides of the thorax and abdomen. Primitively there are twelve segments which may bear spiracles, but there is no known insect which has that number, and only one genus of the Thysanura, *Japyx*, which has eleven pairs. The most common number is ten pairs, two on the thorax and eight on the abdomen. In some of the higher insects there is a reduction in number to six or seven pairs, and some of the abdominal spiracles may migrate to the thoracic region. In the larvae of some forms with complete metamorphosis the number may be still further reduced. Other larvae have neither spiracles nor tracheae, either for a time after hatching or during their whole larval life. One genus of the Collembola, *Smintburus*, is said to have a single pair of spiracles located on the head (Lubbock, 1860).

In most insects the spiracles or the

spiracular trunks immediately behind them are fitted with valves which can be opened or closed. In addition the stigmata are often protected by bristles or hair-like processes. The valves are of two kinds. In the external type the valvular apparatus is an integral part of the spiracle itself, and consists of the two spiracular lips. These are hinged and can be opened or closed by the action of muscles. Such spiracles are always found on the thorax and are larger than those of the second type. Internal valves are located just behind their spiracles on the tracheal trunks leading from them. In the larvae of some of the Diptera the internal valve is merely a sphincter muscle which by contraction occludes the trachea. Most of the higher insects, however, have a well developed apparatus whose construction and method of working was described by Landois (1867). A semicircular chitinous bow extends half way around the trachea. Between the ends of the bow extend a chitinous band and a lever with its muscles. The contraction of this muscle and the action of the lever stretches the bow nearly straight and compresses the trachea, whose elliptical passage is made slit-like. The relaxation of the muscle allows the trachea to open, supposedly by its own elasticity. These spiracular valves evidently serve some function in respiration, since all observers who have described them refer to their periodical opening and closing. In some insects they apparently make certain of the spiracles inspiratory in function by opening during the inspiratory movements of the abdomen and by closing during the expiratory movements. These actions will be further described below.

### THE MECHANICS OF THE RESPIRATORY SYSTEM

No other phase of respiration in the insects has proved so puzzling as has the mechanism of the renewal of the air in the tracheal system, especially in the minute capillaries and tracheoles. This is partly because of the fact that a number of different physiological mechanisms, along with minor structural modifications, have been developed, sometimes within a single order. Aquatic forms have developed several different elaborate modifications of the system to serve for gas exchanges with the water. The matter is further complicated by the modifications which have been introduced in larval and pupal stages and in some nymphs. Often the mechanism in the immature form is quite different from that in the imago. Some idea of the very extensive literature on this subject may be given by the four hundred titles which Babak (1921) quotes in his review of the mechanics of the respiratory system in insects.

The simplest mechanism of gas exchange in the insects is that in a few Thysanura, in certain larvae that live in moist earth or in decaying organic matter, in the early stages of other larvae, and in some parasitic larvae. No tracheae are present in these forms (Palmen, 1877). The exchange of gases between the blood and the outer medium undoubtedly goes on directly through the thin integument. Such forms show but little activity, and presumably do not require a great amount of oxygen for their metabolic processes. A comparable condition is shown in the aquatic larva of *Chironomus*, in which the tracheal system apparently has little or no function in respiration. Hemoglobin is present in the blood of this form. Miall and Hammond (1900) state that the very rudimentary tracheal system appears only late in the larval stage. Fox (1921) investigated the localization of oxygen exchange in larvae of *Chironomus* by the use of the flagellate *Bodo sulcatus*. This

protozoan migrates to a region having a certain optimum oxygen concentration, which is lower than that of ordinary water. Fox found that the larva absorbs oxygen by the whole body surface except the gills and the head. Micro-spectroscopic observations of the gills also failed to show oxidation of the hemoglobin there. It may be that the larva in its burrow makes more use of its gills than the above observations would indicate. It is difficult to see, however, that its tracheal system could be of any use whatever in respiration.

The next degree of complexity of the mechanism is that exhibited by most larvae, by pupae, and by some small imaginal forms, in which respiratory movements are lacking. True respiratory movements are also absent in the Arachnida and the Myriapoda. Diffusion alone, through the open spiracles and the tracheal tubes, must serve in these instances. Krogh (1920) has shown that the wood boring larvae of *Cossus*, a moth, exhibit no true respiratory movements, and has demonstrated directly that an adequate diffusion of oxygen into the tracheal system occurs. Over one spiracle was placed a short tube connected to a second horizontal tube in which a drop of oil served as an index of volume. The drop of oil showed a steady movement toward the spiracle due to a diminution of the enclosed quantity of air as a result of the oxygen consumption in the animal.

### RESPIRATORY MOVEMENTS

In most of the insects, and especially in those with well developed powers of flight, the ventilation of the system is assisted by rhythmical movements of the abdomen. Plateau (1884) has given us the classical description of the movements in many insects. He placed the living insect in a stereopticon lantern and traced the outlines of the enlarged shadow on a screen. In general, the inspiratory movements consist of the expansion of the abdomen. The movements of the head and thorax which may sometimes be observed in some insects are probably only passive and are the results of pressure changes. The expiratory movements consist of the contraction of the abdomen either vertically or transversely. In the Aculeate Hymenoptera longitudinal movements of the abdomen occur together with vertical movements. The vertical movements are always present, and are the more effective. The expansion and contraction of the abdomen are associated with an increase and decrease in the volume of the abdominal cavity. Each abdominal segment is composed of a large tergal or dorsal plate, covering the ventral surface. In some forms the sternum covers more of the sides than does the tergum, and in other forms the two cover the sides about equally. A flexible pleural membrane connects the edges of the tergum and sternum. The terga bear the spiracles in the lower anterior margin. In some insects, such as the Coleoptera, Hemiptera and Blattidae, the rigid sterna yield but little, and the greater movements are made by the thinner terga. In the Odonata, Diptera, Hymenoptera and Acrididae of the Orthoptera, the terga are better developed and fit over the sterna like the lid of a box. Most of the movement is allowed by the membranes, which fold in at contraction and straighten out at expansion. In the Lepidoptera, Neuroptera and Locustidae of the Orthoptera, there is a space between the sterna and terga that is closed by the pleural membranes. At expiration the sterna and terga approach each other, folding the pleura.

It was formerly held that only the expiratory movements are caused by

muscular contraction. Inspiration was supposed to be purely passive, caused by the elasticity of the body wall. It is possible that in some insects, such as the cockroach, the elasticity of the distorted chitinous arcs would cause them to return to their original shape. In many insects, however, it can easily be observed that no such distortion occurs. It is now known that in the Hymenoptera, Diptera, Trichoptera and many of the Orthoptera, inspiratory muscles are present. In the grasshopper, for example, on either side of the sternum of each abdominal segment, an apodeme, or chitinous projection, extends up into the abdominal cavity. Muscles extend from the distal or dorsal end of this apodeme to the ventral edge of the corresponding tergum. Contraction of these muscles separates the sterna and terga, and enlarges the abdominal cavity.

It seems altogether likely that inspiratory muscles will be found in many other groups. In some of the aquatic beetles and Hemiptera, for example, which are known to exhibit respiratory movements, it would appear impossible for inspiration to occur against the hydrostatic pressure without active muscular exertion. It also seems impossible for the nymphs of Anisopterid dragonflies to take a sufficient quantity of water into the rectum merely by passive expansion. Further, there is a physico-chemical objection to the idea that the gas in the tracheal system is compressed by the contraction of the abdomen, and that it causes the passive expansion of the abdomen when the muscles relax. The air in the tracheal system must be at all times under a pressure not much different from atmospheric, since the tensions of the gases dissolved in the water are in equilibrium with the partial pressures of the atmosphere. If the pressure of the air in the tracheal system were greater than the tension of the dissolved air, the system would lose gas through the gills, rather than gain it. The hydrostatic pressure on the outside of the abdomen tending to collapse it is considerable, since the larvae may live at a depth of five meters (Muttkowski, 1918). It is difficult to imagine how the abdomen could enlarge passively without muscular effort against such a hydrostatic pressure. According to Tillyard (1917) the respiratory movements are vigorous and a large volume of water is drawn in rather quickly.

### THE RENEWAL OF THE TRACHEAL AIR

The older idea of the ventilation of the tracheal system was that a tidal inflow and outflow of air through all of the spiracles occurred. Landois (1867) believed that there was an injection of air into the finest tracheal branches by pressure caused by the contraction of the abdomen and the simultaneous closing of all of the spiracular outlets of the system. The physical impossibilities of such a mechanism are obvious, and the explanation was never generally accepted. In a number of insects a sort of circulation of air through parts of the tracheal system has been demonstrated. Certain spiracles, as a result of their valvular actions, function normally only for inspiration and others only for expiration. Brocher (1909, 1911, 1912) has shown that in the Dytiscidae the seventh and especially the eighth pairs of abdominal spiracles are inspiratory, while the other six abdominal pairs serve chiefly for expiration. In the Notonectidae, only the last pair of spiracles are inspiratory. In *Hydrophilus*, according to Brocher, all of the abdominal spiracles are inspiratory except the last pair, which are expiratory. In the Orthoptera, the two pairs of thoracic and the first one or two pairs of abdominal spiracles open during

the inspiratory phase of respiration, and close during the expiratory phase (Lee, 1925). The last six pairs of abdominal spiracles are open during expiration and closed during inspiration. Most of the expired air comes from the last or tenth pair of spiracles. The air thus traverses the longitudinal tracheal trunks from the thorax to the end of the abdomen. The mechanism may be easily demonstrated and expired air collected by thrusting the abdomen of the insect through a hole in a piece of rubber dam covering the mouth of a vial filled with a suitable liquid, and allowing the expired air to displace the liquid. In *Dixippus*, a European species of the Phasmidae or walking sticks, Buddenbrock and Rohr (1923) found that the thoracic spiracles open during expiration and close during inspiration, thus, apparently, allowing a circulation of air from behind forwards. In another Phasmid, *Diapheromera femorata*, the opposite action has been found (Lee, 1927), the thoracic spiracles being normally inspiratory in function. It may be that the action is different in the two species, or the difference may be due to the fact that Buddenbrock and Rohr used partially asphyxiated animals. The normal respiratory movements of *Dixippus* were so slight that they placed the animal under water for a few minutes in order to obtain dyspneic movements. It is altogether likely that under such conditions the normal action of the spiracular valves might be changed.

Such a circulation of air as that just described could, at the most, serve to ventilate only the main longitudinal and cross trunks of the tracheal system. For the renewal of the gases in the smaller tracheae and in the capillaries and tracheoles other mechanisms must be sought. It is probable that the process of diffusion, or a combination of this process with the action of the air sacs, provides an adequate explanation of the ventilation of even the remotest parts of the tracheal tree. Winterstein (1921) has expressed doubts as to the possibility of diffusion through the long, narrow and tortuous tracheal tubes being able to suppy an adequate amount of oxygen, especially during activity. He says (pp. 111–112):

> Wenn man bedenkt, dasz trotz einer relativ vollkommenen Atmungsmechanik in einen Organ von leicht und ausgiebig veränderlichem Volumen, wie es die Säugetierlunge ist, die Alveolarluft sich sowohl in ihrem Sauerstoff- wie in ihrem Kohlensäuregehalt um mehrere Prozent von dem der äuszeren Luft unterscheidet, dann erscheint es kaum faszbar, wie auch durch sehr ausgiebige Atembewegungen in einem System dünner und ziemlich starrer Röhren, deren feinste Ausläufer an der Grenze des mikroskopisch Wahrnehmbaren liegen, eine genügende Erneuerung des Gasinhaltes bewirkt werden kann.

Krogh (1920) has stated his position thus:

> Die chitinösen Tracheen . . . . . sind gewöhnlich von zirkulärem Querschnitt und mit einer spiraligen Verstärkungsleiste—dem Spiralfaden—ausgestattet. Durch diese Struktur wie im allgemeinen durch ihre kleinen Dimensionen setzen die Tracheendem Zusammenpressen durch Druck einen sehr bedeutenden Widerstand entgegen, und eine einigermassen ausgiebige mechanische Ventilation des Tracheensystems wird offenbar schwerlich zustande kommen. Andererseits ist es sehr schwer einzusehen, wie eine unvollständige Kompression des Tracheensystems eine Erneuerung der Luft in den feinen Endzweigen bewirken könnte, und man muss zugeben, dass eine befriedigende Erklärung des Respirationsmechanismus der Tracheaten bisher fehlt.

The theoretical difficulties of diffusion alone serving to supply oxygen to the tracheal end branches led Krogh to put the problem to experimental test. He was able to show that in a number of forms, when at rest, diffusion was able to furnish an adequate supply of oxygen to the tissues. Krogh (1913) first made a study of the composition of the gases in the tracheae of the jumping legs of the grass-

hopper, in order to determine the rapidity and completeness of the exchange of gases in these tracheae with the outside air. A leg was clamped off close to the body, removed and submerged in glycerine. A bubble of gas from the tracheae of the leg was then forced out into the glycerine and analyzed. The legs of other grasshoppers that had been fatigued to exhaustion were treated in the same way. The average results, corrected for systematic experimental errors, were as follows:

| | *Resting per cent* | *Fatigued per cent* |
|---|---|---|
| $CO_2$ | 2.5 | 5.0 |
| $O_2$ | 15.5 | 5.0 |
| $N_2$ | 82.0 | 90.0 |
| Apparent R.Q. | 0.4 | 0.26 |

Since in both the resting and the fatigued legs the carbon dioxide content of the tracheal gas was much less than the oxygen deficit, it must be that a considerable proportion of the carbon dioxide is carried away by the blood, in which it is freely soluble. This is, of course, on the justifiable assumption that the apparent respiratory quotient is much lower than the true metabolic one.

Krogh next placed grasshoppers in an atmosphere containing only oxygen and carbon dioxide, until no nitrogen remained in the tracheae. The animals were then removed to ordinary air and the length of time determined for the normal nitrogen content of the tracheae to be restored. After only one second there was 2.5 per cent of nitrogen in the tracheae, and after only fifteen seconds, or nine respirations, there was 60 per cent. Restoration was complete within one minute. Krogh estimates that about 20 per cent of the air in the leg is replaced by pure atmospheric air at each respiration. This would indicate that the combination of respiratory movements and diffusion is surprisingly efficient in rapidly ventilating even the very small tracheal branches. Analyses of gases from the hind legs of locusts, scarab beetles and ground beetles indicated a close parallel between the efficiency of the respiratory mechanisms and the amount of activity ordinarily manifested by the animal.

Krogh (1920) has further investigated the factors affecting diffusion, using forms (larvae of *Cossus* and *Aeschna*) in which mechanical ventilation of the tracheae could play no part. At the inner ends of the tracheal tubes, where the absorption of oxygen is going on, there will be a partial pressure of that gas less than its partial pressure in the atmosphere. As a result of this difference in tension, oxygen will diffuse inwards. The amount ($S$) which will move in per second will be proportional to the difference in the oxygen partial pressures in the atmosphere and tracheoles ($p - p_1$), and to the cross section area ($A$), and inversely proportional to the tube length ($L$). Or,

$$S = k \frac{(p - p_1) A}{L}$$

$k$ is the proportionality constant, which for oxygen and ordinary temperature is about 0.18 for the selected units. Krogh made the necessary measurements of the oxygen consumption per second, $S$, the cross section area of the tracheae, $A$, and their average length, $L$. The difference in pressure, $(p - p_1)$, necessary for the diffusion could then be calculated. This difference in pressure was found to be 0.13 per cent of an atmosphere for the myriapod *Scutigera*, 2.2 per cent in *Tenebrio* larvae, 2 per cent in *Cossus* larvae, 1.7 per cent in *Lasiocampa* larvae, and 6.2 per cent in *Aeschna* nymphs. Krogh then measured, in an ingenious way, the actual oxygen tension within the tracheal system in *Cossus* larvae. A few spiracles were left exposed to the air and small bells

of collodion were sealed over the others. After a sufficient period of time for equilibrium, the gas in the bells should be of the same composition as that in the tracheal system. Analyses of this gas showed oxygen tensions lower than the oxygen tension of the atmosphere by amounts in very close agreement with those calculated by the above formula.

By the use of Krogh's microrespiration methods, Buddenbrock and Rohr (1923) showed that the closure of all of the spiracular openings in *Dixippus* reduces the respiratory exchange about three-fourths. The gas exchange directly through the integument in this form is thus about one-fourth of the ordinary resting rate. The oxygen tension of the tissues was found to be about 10 per cent of an atmosphere. The reduction of the oxygen content of the air down to 10 per cent had no effect, as would be expected. Below this concentration of oxygen the respiratory movements increased in frequency and amplitude.

It would appear to have been conclusively demonstrated that the process of diffusion alone is sufficient for an adequate gas exchange in the great majority of larvae, all pupae, and in the smaller and comparatively lethargic adult insects. In the larger, more active forms, and especially in those with well developed powers of flight, the process of diffusion alone must be inadequate. Krogh himself has pointed out, that as the size of the insect increases, diffusion remains proportional to the linear dimensions, while weight increases as the cube of the linear dimension, and the resting oxygen consumption increases at a rate between the square and the cube of the linear dimension. The oxygen consumption of the higher insects, even when at rest, is much above that of the less active smaller forms. In the honey bee an oxygen consumption of 20,000 cc. per kilogram per hour has been observed (Parhon, 1909). During flight the oxygen consumption must be much greater than this. For such a consumption diffusion alone will not suffice, as Krogh has emphasized, even if the body weight is only 0.1 gram. In this connection a possible function of the air sacs may be considered.

### THE AIR SACS

Air sacs are found in most of the winged insects, and in many of the non-flying forms. They are simple, elastic, epithelial-lined dilatations of the tracheae, usually without the intimal layer. They vary greatly in size, number and distribution in the various groups. In fact, they show a parallel development with the powers of flight and in some of the most successful of the flying insects they may together occupy as much space as the alimentary canal. It is not generally realized how great their number may be in an insect. Landois (1867) states that the number in the male of *Melolontha vulgaris* is around 550, many of which approach a diameter of 2 mm. Alt (1912) has described the veritable complex of air sacs in the thorax and abdomen of *Dytiscus marginalis*. Packard (1878) has counted fifty-three sacs in the head alone of *Melanoplus femur-rubrum*. Vinal (1919) has described the extensive air-sac system of the Carolina locust, *Dissosteira*, and his illustrations show small air sacs in the large jumping legs. According to Newport (1851) there are air sacs even in the mandibles of the stag beetle. It is especially noteworthy, in view of their possible function, that many of the sacs arise from the smaller tracheal branches at a considerable distance from any spiracles. Even the largest ones do not open immediately off of the large spiracular trunks, but usually from some of the longitudinal

trunks. They are located all through the body, the large ones usually directly beneath the hypodermis, while the smaller ones may be buried among the muscles. Miall (1903) has described dilatations in the tracheae of the larva of *Ptychoptera* which can be expanded like air sacs and MacGillivray (1903) has described air reservoirs in the aquatic larva of *Donacia*. The sacs are not blind pockets at the ends of tracheal tubes, but usually have many efferent branches, which are very short as compared with the total length of the tracheal tree.

Up to the present time, the functions of the air sacs have been far from convincingly described. Two different functions have been ascribed to them. Newport (1851) observed their number and size in the rapidly flying insects, and was led to the naïve belief that they serve for buoyancy during flight by lessening the specific gravity of the body. Newport believed that the air sacs in the birds serve the same function. It is of course true that the specific gravity with respect to water, of the body as a whole would be lessened, but the weight to be supported by the wings would be just as great whatever the expansion of the body, and the greater air resistance and unwieldiness of the larger bulk would be a disadvantage. It is quite possible that the air within the sacs is at slightly higher temperature than the outside air, but the buoyant effect from such a cause would be inconsiderable. It is possible that an increased size of skeleton may be advantageous for the attachment of muscles. Larger flies, for example, have greater powers of flight than do the small ones. It is certainly true that in the birds the respiratory function of the air sacs in ventilating the lungs is by far their most important one.

The other view which has been held regarding the function of the air sacs is that they are simply reservoirs of air, especially developed in the flying insects because these forms consume a great deal of oxygen in flight. There are a number of reasons for rejecting such a simple explanation. There would seem to be no advantage to an insect in having air reservoirs within the body when the whole atmosphere is a reservoir just a few millimeters away through the open spiracles. The amount of air in the sacs could hardly serve as a source of oxygen for very long, unless constantly renewed, since the total volume of the sacs is small compared with the volume of air the animal uses in an hour, and less than 20 per cent of the gas is oxygen. If the functions of the sacs were either for buoyancy or as a reservoir there would seem to be little reason for having 550 small sacs, as is the case in *Melolontha*, rather than a few large ones.

It would appear that another explanation, almost self-evident, would account not only for the presence of the air sacs, but for their parallel development with the powers of flight. This explanation is that their function is chiefly mechanical, in allowing a considerable volume of air to be inhaled and exhaled (Lee, 1928). The mechanism will be made clear if one imagines the body of an insect as containing no air sacs at all. The ordinary tracheae offer considerable resistance to pressure tending to collapse them. Neither can they be distended to any appreciable extent. They are elastic only in that if they are distorted out of round by pressure they will return to their original shape when the pressure is removed. The spiral taenidial threads would appear to be especially effective in preventing either collapse or distension. The cavities of the insect's body have no connection with the lumen of the tracheae.

Therefore, in such an insect without air sacs, both the inspiration and expiration of air would be absolutely impossible.

With air sacs present, whether a few large ones or many small ones, the situation is entirely different. In so far as the mechanics of respiration are concerned, the insect could be compared in a number of respects with the bird or mammal. The hemocoele of the insect would be analogous with the whole body cavity of the bird or the thoracic cavity of the mammal. The active expansion of the abdomen of the insect would be analogous with the increase in size of the body cavity in the bird or of the thoracic cavity in the mammals. During the expansion of the abdomen the hemocoele becomes larger and the intracoelomic pressure must decrease. As soon as this intracoelomic pressure becomes less than atmospheric, the air, having free access to the tracheal system through the spiracles, will dilate and fill the thin walled elastic air sacs, wherever they are located. During expiration, the abdomen is compressed and made smaller, the intracoelomic pressure is increased above atmospheric, and this pressure, transmitted by the blood to all parts of the body, will cause the air sacs to collapse and empty themselves. The greater the total capacity of the air sacs, the greater would be the possible ventilation in a single respiration. The pressure causing the alternate dilatation and collapse of the air sacs is first the pressure of the outside atmosphere and then the blood or intracoelomic pressure.

If such a conception of the function of the air sacs is correct, there would be an enormous advantage in having a great number of small air sacs scattered throughout the body, rather than a few large ones. Each sac would serve to ventilate the section of tracheal tube between it and the nearest open spiracle. The agitation given to the tortuous column of air should be very effective indeed in aiding the diffusion of oxygen. It has long been a puzzling question how the organs in the head of an insect, far removed from the spiracles, could get by diffusion enough oxygen to supply their needs. With this view of the function of the air sacs the difficulty disappears. The changes in intracoelomic pressure will be transmitted by the blood to the air sacs of the head as well as to any others, and cause the alternate collapse and dilatation. The work of Krogh, reviewed above, would indicate that for the comparatively short distance between the air sacs and the terminal tracheal capillaries, the process of diffusion alone would supply an adequate amount of oxygen for the needs of even the most active insects. The parallel development of the air-sac system with the powers of flight would indicate the efficiency of the mechanism for supplying an adequate gas exchange for such an energy consuming activity.

Such a view of the respiratory action of the air sacs implies that inspiration is an active muscular act. During inspiration there must be a decrease in the intracoelomic pressure to below atmospheric for any distension of the air sacs to occur. It is difficult to see how the abdomen could expand passively against a positive atmospheric pressure. The presence of inspiratory muscles in a number of groups has been noted above. Such muscles may be found in other groups, or the elasticity of the chitinous arcs of the abdominal wall, distorted during expiration, may be great enough to cause, in returning to their original shape, a partial vacuum in the abdomen.

The changes of pressure in the air sacs of the grasshopper, *Melanoplus differentialis*, may easily be demonstrated by watching the sacs through the transparent conjunc-

tivae under the wings on the mesonotum and metanotum. The wings should be pulled back or cut away. At each contraction of the abdomen the thin conjunctivae will be seen to distend and the air sacs beneath them may be seen, dilated at first, then gradually emptying. Upon the expansion of the abdomen or during inspiration the conjunctivae will be seen to be pressed inwards by the atmospheric pressure, and the air sacs may be seen to dilate and fill at the same time.

### THE LOSS OF CARBON DIOXIDE

The elimination of the carbon dioxide produced in the body of the insect is less difficult of explanation than is the supplying of oxygen. Any mechanism which adequately explains the renewal of the oxygen supply in the capillaries and tracheoles will also account for the loss of carbon dioxide. Numerous analyses of the air expired from the tracheal system in various insects have shown that the carbon dioxide content is from two to five per cent. Although in many cases this amount is considerably less than the oxygen deficit, it is undoubtedly true that the greatest part of the carbon dioxide exchange is by way of the tracheae. Accessory mechanisms, however, may account for a significant part of the total loss. Buddenbrock and Rohr (1923) state that about one-fourth of the ordinary gas exchange in *Dixippus* occurs directly through the integument. It has been suggested that in ecdysis, especially at the end of pupation, accumulated carbon dioxide is lost, both as carbonate in the old skeleton and as gas directly through the new soft chitin.

### RESPIRATORY PIGMENTS

The respiratory pigments hemocyanin, hemoglobin, chlorocruorin and others have been found in the blood of many of the invertebrates, and it has been thought that the blood of the insects might contain some such chromoprotein. The larvae of some of the harlequin flies, Chironomidae, were shown by Rollett (1861) and Lankester (1873) to have hemoglobin in their blood. These larvae often live under more or less anaerobic conditions, such as are found in the deeper waters of lakes and in thermal springs (Brues, 1927). Miall and Hammond (1900) considered that the hemoglobin in the larva of *Chironomus* is employed as a store for oxygen, rather than as a transport mechanism. Leitch (1916) has shown that such a view is untenable. The quiet larva uses about 2.675 milligrams of oxygen per gram of body weight per minute. At such a rate of consumption the hemoglobin could serve as a store of oxygen for a maximum of about twelve minutes, rather than for several days as Miall thought. According to Leitch the larvae do not utilize their hemoglobin unless the oxygen tension of the water is below seven millimeters. At tensions above this the oxygen in physical solution in the blood is sufficient for the needs of the body and is renewed rapidly enough from the water that the hemoglobin does not dissociate. She believes that the function of the hemoglobin consists in making available by its power of binding oxygen chemically, a quantity of oxygen sufficient for the needs of the larva, at oxygen tensions so low that the necessary amount is not supplied by physical solution.

Muttkowski (1921) has shown the presence of copper in the blood of all of the insects he studied, thirty-four species, representing all of the chief orders. Quantitative determinations were not made. The tests indicated, however, that the copper was present in amounts comparable to that in crayfish blood.

In many of the Crustacea copper has been shown to be the nucleus of the respiratory pigment hemocyanin. Muttkowski believes that the copper in insects' blood is similarly a part of a respiratory pigment and that the blood of an insect has a respiratory function strictly comparable to that of the blood of the vertebrates. The presence of such a chromoprotein would help to explain the apparent efficiency of the blood gills found in a number of aquatic forms. The problem is an interesting and important one, and it would appear well worth while to put on an experimental and quantitative basis the possible rôle of copper in a respiratory pigment in insect blood. As to the properties of hemocyanin and the nature of its union with oxygen, there have been many conflicting reports. In a late careful investigation Redfield, Coolidge and Hard (1926) have demonstrated that the hemocyanins of four marine invertebrates, *Limulus*, *Loligo*, *Busycon*, and *Cancer*, function in the transport of oxygen and carbon dioxide according to the same physicochemical principles as obtain in the case of hemoglobin.

### THE CONTROL OF RESPIRATION

Bethe (1897) and Ewing (1904) have studied the nervous control of respiration in some of the insects. In the Orthoptera, and probably in most of the higher insects, each ventral ganglion of the abdominal chain is the center for the respiratory movements of its segment. Respiration continues after decapitation, and sections of the abdomen of only one or two segments will exhibit respiratory movements for some time. Each ganglion also controls the movements of the spiracular valves in the segment to which it belongs. Ewing removed the thoracic ganglia of grasshoppers and found that the thoracic spiracles were paralyzed. Faivre (1875) thought that the thoracic ganglia were the only respiratory centers in *Dytiscus*, but this work has not been confirmed.

In addition to this segmental arrangement there obviously must be an additional or supplementary mechanism for the correlation of the movements of the various segments. This is especially true for the movements of the spiracular valves in the forms in which they are opposite in action in the thorax and abdomen. It would seem that the question of both nervous and chemical control of respiration in insects would well repay further extended investigation.

Carbon dioxide is a specific stimulus to the respiratory center in the mammals. It is doubtful whether it is such a stimulus to the centers in the insects. Babak and Foustka (1907) consider that oxygen lack in some way causes stimuli promoting respiratory movements in dragonfly nymphs. They found that if the water were very poor in oxygen, a typical dyspnea appeared. In water saturated with oxygen and covered with an atmosphere of pure oxygen, long periods of apnea occurred. Changes in the concentration of carbon dioxide had no such effect upon the respiratory rhythm. Buddenbrock and Rohr (1923) observed that when the oxygen content of the air was reduced to 3 or 4 per cent, the respiratory movements of *Dixippus*, which are ordinarily very slight, become energetic.

### RESPIRATION IN AQUATIC FORMS

Complicated as is the mechanism of respiration in the insects, it is still more complex in the many aquatic forms. Here mechanisms originally developed for air respiration on land, have been secondarily modified to function in water. So far as is known all water inhabiting insects are descended from terrestrial forms and are only secondarily aquatic.

The number of species that have taken up life in the water is surprisingly large. If permanent adaptations to all sorts of environments be one measure of biological success, then the insects must be placed above all other groups in this respect. It is probable that in several orders a number of separate changes to aquatic life have been made and quite different mechanisms for gas exchange have been developed. There are, too, all degrees in the completeness and efficacy of the modifications for respiration. In the aquatic environment there are many different habitats involving very different conditions of oxygen supply. Some habitats are almost lacking in oxygen; in others the oxygen tension, due to green water plants, is greater than the oxygen tension of the atmosphere. Insects may be found under almost all of these conditions, wherever food may be found.

The holopneustic forms, or those with open functional spiracles, are wholly or partially independent of the dissolved oxygen of the water. They breathe at the surface, carry a supply of air below with them or utilize the air stores in the stems or leaves of water plants. As might be expected, their respiratory mechanisms are essentially the same as those of terrestrial forms. In aquatic insects which have an apneustic or closed spiracle system, but which depend upon the tracheal system for the distribution of oxygen from the gills to the tissues, the bodily movements can probably be of little or no aid in helping the mixing of the gas within the tracheae. The tracheal gas must be under approximately atmospheric pressure, or less, since it is in equilibrium with the gas dissolved in the water. The actual pressure on the tracheal tubes tending to collapse them, however, may be considerably more than atmospheric. Dragonfly nymphs, for example, may live at a depth of 4 to 5 meters. The total outside pressure may thus be upwards of 1.4 atmospheres. The tracheal tubes must be able to withstand such a pressure without transmitting it to their contained air. Otherwise there would be a steady loss of the gas through the gills to the water and the end result would be the complete emptying and collapse of the tracheae.

The following table lists the more common forms of aquatic insects, and the mechanisms used for gas exchange in each case.

The work on the respiratory mechanisms in the larvae of the Odonata has been reviewed by Tillyard (1917). Most of these larvae are carnivorous and predacious and show considerable activity in the water. They are found in a wide range of habitats, varying from swiftly running water to swamps and bogs, and from shallow water to deep. In the larvae of the Anisoptera, the anterior two thirds of the rectum is expanded into a barrel-like chamber, the branchial basket. From the walls of this chamber six longitudinal sets of gills project into the lumen. Each gill is abundantly supplied with tracheal branches and capillaries and from 10,000 to 90,000 tracheolar loops. By the respiratory movements of the abdomen, water is alternately drawn into and expelled from the rectum. According to Krogh (1920) the nymph of *Aeschna* consumes about 300 cc. of oxygen per kilogram per hour, an amount which can easily be supplied by diffusion from the water into the tracheal system and to the tissues.

In the Zygopterid larvae, the caudal and lateral tracheal gills are waved to and fro in the water and probably serve for gas exchange. If these gills are lost, however, the larva is still able to live. The rectum presumably serves also for respira-

COMMON AQUATIC INSECTS

| GROUP | AQUATIC STAGE | METHOD OF RESPIRATION |
|---|---|---|
| Odonata | Nymphs of all species | |
| Anisoptera | | Tracheal gills in anterior portion of rectum. |
| Zygoptera | | Caudal tracheal gills in most. In some, lateral tracheal abdominal gills. Blood gills in rectum. |
| Trichoptera | Nymphs of all species | Lateral abdominal tracheal gills. Blood gills in some. |
| Ephemerida | Nymphs of all species | At first through integument only; later by lateral tracheal gills, usually on abdomen only but on thorax in some forms. Rectal blood gills. |
| Plecoptera | Larvae of all species | Caudal tracheal gills in most forms. Thoracic tracheal gills in a few. |
| | A few adults | Caudal tracheal gills much like those of the larva. |
| Neuroptera | | |
| Hemerobidae | Larvae | Caudal tracheal gills. |
| Sialidae | Larvae | Lateral abdominal tracheal gills. |
| Corydalidae | Larvae | Lateral abdominal tracheal gills. |
| Hemiptera | | |
| Corixidae | Nymphs and adults | Air breathing at surface. Air store carried below by hydrofuge hairs. |
| Nepidae | Nymphs and adults | Air breathing through long tubes at end of abdomen. |
| Notonectidae | Nymphs and adults | Air breathing at surface. Air film around body when submerged. |
| Belostomidae | Nymphs and adults | Air breathing. Tip of abdomen thrust through surface. Floats head downwards. |
| Coleoptera | | |
| Hydrophilidae | Larvae | Spiracles at tip of abdomen. |
| | Adults | Air space between elytra and abdomen. Also air film under abdomen. |
| Gyrinidae | Larvae | Lateral and caudal tracheal gills. |
| | Adults | Air bubble carried at tip of abdomen when submerged. |
| Dytiscidae | Larvae | Air breathing by two spiracles at tip of abdomen. |
| | Adults | Air store between elytra and abdomen. |
| *Hydrobius* | Larvae | Spiracles at end of abdomen; air bubble carried below surface; short lateral gills. |
| | Adults | Air store under elytra and film of air around abdomen. |
| Chrysomelidae | | |
| *Donacia* | Larvae | Spines, which are thrust into air cavities of water plants, form a tube through which air is obtained. |
| *Haemonia* | Adults | Air stores around abdomen. |
| *Pelobius* | Larvae | Lateral abdominal blood gills. |
| Haliplidae | Adults | Air stores around abdomen. |
| Lepidoptera | | |
| *Nymphula* | Larvae | Through integument only in some; by tracheal gill filaments in some; in others by combination tracheal-blood gills. |
| *Cataclysta* | Larvae | Blood gills. |
| Hymenoptera | Larvae of a few small parasitic forms | Directly through integument. |

| GROUP | AQUATIC STAGE | METHOD OF RESPIRATION |
|---|---|---|
| Diptera | | |
| Psychodidae | Some larvae | Caudal tracheal gills; caudal spiracles; air bubble carried below surface. |
| Corethridae | Larvae | Through integument. Imperfect tracheal system. |
| | Pupae | Respiratory tubes from head to surface of water. |
| Chironomidae | Larvae | Through integument: hemoglobin in blood. |
| | Pupae | Respiratory filaments from prothorax. |
| Blepharoceridae | Larvae | Ventral abdominal tracheal gills. |
| Culicidae | Larvae | Respiratory tube from end of abdomen to surface. Also rectal respiration. |
| | Pupae | Two respiratory tubes from back of thorax. Hangs from surface film. |
| Stratiomyidae | Larvae | Spiracles at end of elongated abdomen. Hangs from surface film. |
| | Pupae | Floats on surface of water. |
| Tipulidae | Some larvae | Through integument. |
| Syrphidae | Larvae | Long caudal tube to surface. |
| Simulidae | Larvae | Respiratory filaments from head. Lives in swiftly flowing streams. |
| | Pupae | Respiratory filaments from head. |
| Dixidae | Larvae | Spiracles at tip of abdomen, which is thrust through surface film. |
| | Pupae | Respiratory tubes on thorax. |

tion, although it contains no true tracheal gills. The same situation exists in the Ephemerida, the lateral tracheal gills being supplemented by the rectum.

It is generally agreed that Odonate larvae were once air breathing forms (Dewitz, 1890). Krogh (1920) considers it most likely that the nymphs of the enormous dragonflies of Carboniferous time must have had an open tracheal system and mechanical respiration. The adults were approximately 30 cms. long and 0.3 cms. wide. Krogh has calculated that diffusion alone could not possibly supply enough oxygen in such large forms.

Little is known of the physiology of respiration in the aquatic larvae of the Trichoptera, Plecoptera, Megaloptera and Neuroptera. All of these forms possess tracheal gills, either lateral or caudal. It is inferred that gas exchange takes place chiefly through these structures, much as in the Zygoptera of the Odonata.

Welch (1922) has studied the respiratory mechanisms in aquatic Lepidoptera larvae of the genera *Nymphula* and *Cataclysta*. In both of these genera there are species with gills and species without them and no known intergrades. In both the gilled and non-gilled forms the tracheal system is of the holopneustic type, that is, the spiracles and connecting tracheae are morphologically open. In the non-gilled types, respiration is either carried on between the blood and the water through the body wall or else the larva ascends to the surface and opens its spiracles. In the gilled types there are gills of two different kinds—tracheal blood gills, the more complex, in which there are both tracheae and blood, and blood gills in which blood only is found. The tracheation of the body is practically unmodified from that of terrestrial forms.

The air stores carried beneath the surface of the water by some of the large

diving beetles and bugs probably have a hydrostatic as well as a respiratory function, and serve to bring the animal to the surface whenever the swimming movements are stopped or the hold on vegetation is released. Brocher (1909, 1911, 1912) demonstrated such a hydrostatic function for the air stores of the Corixidae, Dytiscidae, Hydrophilidae, and Notonectidae. He considered that the air stores have no respiratory function, since he could not demonstrate that the animals made respiratory movements while submerged. However, Babak (1912) and van der Hyde (1922) have shown that respiratory movements do occur in *Dytiscus* while beneath the surface, and Ege (1918) and van der Hyde have shown by gas analysis that the oxygen of the supply is consumed during the stay under water. In studying the mechanism of breathing in *Dytiscus*, van der Hyde observed the movements of a droplet of petroleum when the animal was allowed to breathe in a space closed by this droplet. Inspiratory and expiratory movements, both when the animal was submerged and when it was at the surface, were recorded by the droplet. When the beetle comes to the surface the end of the abdomen pushes through the surface film. The two elytra are then slightly raised and the large space between the back of the abdomen and the elytra is put into free communication with the atmospheric air. Supposedly the air is renewed. The edge of the abdomen is waxy and water does not enter the dorsal space. After the beetle has opened its elytra at the surface there is a short pause, followed by an expiration from the spiracles. Immediately after the expiration the animal usually dives. Analysis of the air store soon after diving showed 0.65 per cent of carbon dioxide, 14.01 per cent of oxygen and 85.34 per cent of nitrogen. After being submerged for some time the analysis showed 0.64 per cent carbon dioxide, 3.05 per cent oxygen and 96.31 per cent nitrogen.

Ege (1918) considers that the air stores have a respiratory function, but not that usually accepted. He believes that the air stores enable the holopneustic animal to utilize the dissolved oxygen of the water. When the oxygen tension in the air store becomes less than that in the surrounding water, oxygen will diffuse into the store, the rate depending upon the tension difference and the area of the free surface for diffusion. The carbon dioxide produced by the animal will diffuse out in the same way, but at a much faster rate than the oxygen diffuses in. The proportion of nitrogen in the store will thus tend to accumulate and will acquire a partial pressure greater than the tension of nitrogen in the surrounding water. The nitrogen will then diffuse out, the volume of the store will be decreased, and no more oxygen can be obtained from the water. Ege considers that the beetle comes to the surface chiefly to renew the supply of nitrogen.

It seems probable that Ege's idea of the action of the air store, while correct theoretically, is not important practically. The small area offered for diffusion, and hence the slow rates of passage of oxygen and nitrogen into and from the store, make it likely that the oxygen is used up long before there is a marked decrease in the volume of the store. Van der Hyde has calculated the quantity of oxygen which could diffuse into the store to be about 0.52 cubic millimeter per minute. According to Ege's figures, one *Dytiscus* consumes in one minute about 8 cubic millimeters of oxygen. The discrepancy between the amount the animal uses and the amount which could be supplied by the water is evident.

Van der Hyde further studied the rela-

tive importance of the gases in the water and in the air for the animal's behavior by varying the gas content of the water and the composition of the atmosphere. If boiled water is used, the animal goes to the surface more often, presumably because the air in the air store diffuses out and dissolves in the water. But if boiled water was cooled and then saturated with carbon dioxide, the beetle went to the surface less often. In an atmosphere of carbon dioxide above water containing oxygen, the beetle remained at the surface.

In concluding this review it must be repeated that no complete or detailed summary of our knowledge of the process of respiration in insects has been attempted. The large fields of metabolism and the effects of temperature on the respiratory exchange have been touched only casually for illustrative purposes. The attempt has rather been to present some of the fundamental lines of inquiry into the general subject, and to illustrate these with pertinent references to both the older and the more recent literature. The viewpoint has been constantly in mind that the remarkable success of the insects as a group has been conditioned by the development of efficient respiratory mechanisms, adequate for supplying oxygen for the considerable energy releases necessary in active movements and in flight, and adapted for use under the most varied habitat conditions.

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# THE PALAEOMORPHOLOGY OF THE HUMAN HEAD: TEN STRUCTURAL STAGES FROM FISH TO MAN

## PART II. THE SKULL IN NORMA BASALIS

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*American Museum of Natural History*

### INTRODUCTION

IF WE make careful comparisons of the skulls of recent fishes, amphibians, reptiles, birds and mammals, including man, we can hardly fail to recognize either the existence of class types of skull patterns or the gradually changing ground-plan that underlies the entire series; and if we study the separate bones that together make up each of these skulls we readily identify some of the homologous elements throughout the series, while as to other elements the differences among recent forms of different classes may be so great as to leave some uncertainties which even the most intensive purely morphological analysis may fail to clear up. When, however, we extend our comparisons to include both fossil and recent vertebrates of all known orders, experience shows not only that the patterns of the skulls, especially in the side view, afford one of the most reliable sources of evidence as to the relationships of the forms that bore them, but also that the great differences observed between recent forms of the different classes are more or less completely bridged by intermediate conditions which in the end may leave little doubt as to the origin and evolution of such troublesome elements of the mammalian skull as the vomer, the presphenoid, and the great wing of the sphenoid. In short, the history of the evolution of the human skull as here summarized is based upon many general results of modern systematic zoology, palæontology, phylogeny and morphology.

Hence the selection of specimens to illustrate the evolution of the skull from fish to man is not the result of arbitrary choice or preconceived theory on the part of the author. It is the result first, of the labors of all those who have determined the systematic position and phylogenetic relationships not only of the forms that were finally admitted to the series but also of all other forms that might be considered to have claims to stand in or near the line of ascent from fish to man; secondly, each of the series finally adopted for the present purpose was a residuum after the elimination of all other forms which were more specialized than it was, away from the main line of ascent and toward terminal vertebrate forms other than man. Finally, a skull was admitted to the series if its pattern as a whole and in its component parts exhibited one series of characters that plainly foreshadowed the later forms and another that was inherited from earlier stages.

The resulting series doubtless does not constitute a direct phylogenetic series from fish to man, which in practice must ever remain an unattainable ideal, but it does constitute one which leaves little or

no doubt as to the evolutionary history as a whole and as to the main changes of the principal skull elements.

In the present article the history of the norma basalis of the skull is considered. Owing to the great rarity and imperfect preservation of fossil skulls of many of the stages figured in Part I (QUART. REV. BIOL., Vol. II, pp. 267–279. 1927), it is not practicable to show the basal aspects of all the forms used in the side view series. More or less nearly related forms have therefore been substituted, under the condition that their norma basalis is substantially similar to that of the form figured in the series of side views, at least in respect to its supergeneric group characters.

In a general way the elements visible in the norma basalis of the premammalian vertebrate skull may be classified as follows:

I. Jaw elements.
  A. Outer or secondary jaw: comprising dermal elements, the premaxillæ (*pmx*), maxillæ (*mx*), jugals (*ju*) and quadratojugals (*qj*). The jugal also belongs in the circumorbital series and thus has a double function. The quadratojugal is also classified as one of the temporomandibular series in the side view.
  B. Inner or primary jaw: comprising
    1. The pterygoquadrate arch, preformed in cartilage; including the epipterygoids (*ep*), pterygoids (*pt*) and quadrates (*qu*).
    2. The adherent tooth-bearing dermal elements: prevomers (*pv*), palatines (*pl*), pterygoids (*pt*) and ectopterygoids (*ectpt*).

II. Keel bone (parasphenoid, *pas*); originally forming the median dermal base of the cranium, underlying the ethmoid and basisphenoid.
III. Basicranial elements:
  A. Basisphenoid (*bs*), including basipterygoid processes for articulation with the pterygoids.
  B. Basioccipital (*bo*), exoccipital (*eo*).
IV. Temporal element: squamosal (*sq*).
V. Otocranial elements:
  A. Proötic (*pro*);
  B. Opisthotic (paroccipital, *opo*).
VI. Hyobranchial elements:
  A. Stapes (*stp*).

The various openings or fossæ seen in the norma basalis of the vertebrate skull are of great importance as landmarks. They include the following:

(1) Paired internal nares (*nar*);

(2) Interpterygoid fossa, lying between the opposite pterygoids;

(3) Temporo-mandibular fossæ, lying between the jugals and quadratojugals on the outer side, the quadrates behind, the pterygoids medially and the ectopterygoids anteriorly. These openings give passage to the jaw muscles as they pass downward from the temporal fossa to the mandible. They may be traced securely from fish to man.

## REVIEW OF THE TEN STRUCTURAL STAGES IN NORMA BASALIS

### *Stage I. Devonian lobe-finned ganoid, Eusthenopteron*

Figure from Watson, mostly after W. L. Bryant.

The stages leading up to this form are not known, except in so far as the ostracoderms and the sharks illustrate two successive stages in the evolution of the jaws. In the other direction this fish

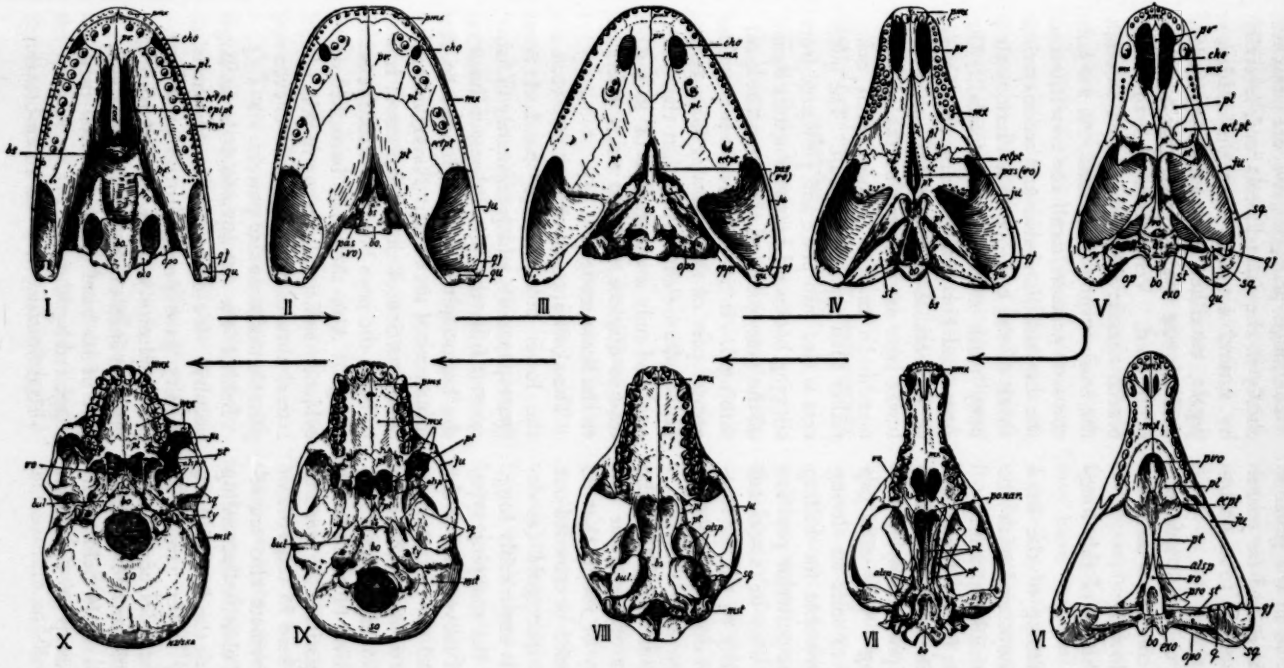


FIG. 1. EVOLUTION OF THE SKULL IN NORMA BASALIS

Stage I. Devonian lobe-finned ganoid, *Eusthenopteron*. Figure from Watson, mostly after W. L. Bryant.
Stage II. Lower Carboniferous embolomerous amphibian, *Eobaphetes*. Figured by Watson.
Stage III. Primitive Permo-Carboniferous reptile, *Seymouria*. Figure from Watson; data from Broili, Williston, Watson.
Stage IV. *Captorhinus*, advanced cotylosaurian reptile of the Permian. Figure and data from specimen. Data also from Broom, von Huene, Sushkin.
Stage V. *Scylacops*, primitive mammal-like reptile of the Middle Permian. Figure and data from Broom.
Stage VI. *Cynidiognathus*, advanced mammal-like reptile of the Triassic. Figure from Broom. Data from Seeley, Haughton, Broom.
Stage VII. *Thylacinus*, modern marsupial mammal, representing a survivor of Cretaceous marsupial stock. Figure and data from specimens.
Stage VIII. *Adapis*, representing Eocene lemuroid primates. Figure and data from Stehlin.
Stage IX. Chimpanzee, representing a little-modified survivor of the Miocene anthropoid stock. Figure and data from specimen.
Stage X. *Homo sapiens*, represented by aboriginal Australian, survivor of Pleistocene man.

already foreshadows man in the ground-plan of its skull and is indeed far nearer to him in essentials than it is to its proto-chordate starting-point.

The general form of this skull has been determined by many conditions and factors, including the following:

(1) the predaceous habits of this long-jawed, snapping fish;

(2) the general flattening of the head and throat, possibly associated with the habit of lying on the muddy bottom.

The articular surfaces for the lower jaw are located far back, immediately behind the plane of the occipital condyle, this arrangement permitting a very wide gap and enabling the fish to seize its living prey in a position favorable for killing and swallowing it. The posterior position of the quadrate may also be associated with the possible ability to tilt the fore-part of the head upward after the fashion of a crocodilian, as suggested by Watson.

In conformity with the length of the jaws, all the elements of the outer and inner jaws have plenty of room, that is, none of them are squeezed or crowded out of existence. The ectopterygoid (as determined by Watson) is remarkably long.

The dentition is of the snapping type, requiring only vertical movements of the mandible. The parallel rows of teeth in the lower jaw alternate and fit between corresponding rows in the upper, the larger, more medial rows of teeth being in the most favorable position for piercing and killing the prey held in the roof of the mouth. The prevomers also are remarkably large and, if classified according to function, belong with the dermal plates covering the primary upper jaw. The pterygoids forming the sides of the roof of the mouth are steeply arched to allow room for the prey as it is held while being killed by the snap of the lower teeth.

The huge primary jaws are attached chiefly to the dermal skull roof, laterally by sutural contacts with the quadrato-jugals, maxillæ, premaxillæ; vertically, through the broad epipterygoids to the skull roof. Ventro-laterally they are braced against the basisphenoid through the basipterygoid processes. As a whole the arrangements recall the conditions in the amphistylic sharks and we may thus think of the crossopt as a shark with a bony mask over its whole head. The jaws need but little bracing against the skull, because the primary upper and lower jaws are squeezed by the adductor mandibulæ muscles against each other rather than against the skull. The quadrate is tied into place and prevented from slipping backward by the quadrate flange of the pterygoid and the sheet-like quadratojugal. It is thus evident that the greater part of the muscular force is expended dorso-ventrally against the pterygoid and only a small part of it would tend to displace the jaw with reference to the brain trough.

The skull appears structurally weak on the lower side because the keel bone (parasphenoid), which ordinarily in fishes extends from the ethmoid region back to the basioccipital, is here limited to the front part of the skull. Nevertheless the chief function of the parasphenoid is not to brace the jaws but to protect the brain trough. Also the small basisphenoid is evidently sufficiently strong to take up the lateral thrusts resulting from uneven application of muscular power.

Behind the parasphenoid is a large vacuity. We do not know whether this vacuity gave passage to an open hypophysio-pituitary tract or whether its presence enabled the fish to raise the fore-part of its head upon the back part (as suggested by Watson).

That *Eusthenopteron* was an air-breathing

fish and therefore possessed a lung, like that of the related dipnoans, is rendered probable by the presence (according to Bryant and Watson) of internal narial openings lying between the premaxillæ, maxillæ and palatines.

In the occipital region of *Eusthenopteron* we note a wide expansion and forward extension of the otic capsules containing the semicircular canals on either side of the occipital segment. The basioccipital is well developed and forms the thrust block between the vertebral column and the skull. The exoccipitals are figured as distinct from the opisthotic.

*Stage II. Lower Carboniferous embolomerous amphibian, Eobaphetes*

Figured by Watson.

In this remarkably primitive amphibian we are impressed by the retention of a fundamentally piscine palate, all the elements of which are directly comparable with that of *Eusthenopteron.*

(1) There is a complete development of both primary and secondary jaws, with all components present, at least as seen from the basal aspect.

(2) The arrangement of the dentition is essentially crossopterygian, with a row of small teeth on the outer jaws and a series of large labyrinthodont tusks on the dermal covering bones of the inner, or primary jaw.

(3) The internal nares open inward, behind the premaxillæ and between the prevomers and the palatine.

(4) There is a restricted movement of the head upon the column, indicated by the truncate basioccipital articular surface.

On the other hand, this primitive amphibian already foreshadows the later tetrapods in the ground-plan of the norma basalis. There is a marked contrast in the position of the parasphenoid, which together with the lateral basipterygoid processes, is now displaced backward nearly to the occiput. We do not fully understand the reasons for this contrast; possibly, as suggested by Watson, the amphibian may be derived from fish other than the rhipidistians, in which the parasphenoid extended backward to the occipital region. Or the basisphenoid may have been pushed backward, due to a possible rearrangement in the position of the eyes consequent upon the change from water-living to amphibious habits. In the amphibians as a rule the eyes lie much farther back than in either the rhipidistians or the dipnoans. Also the olfactory chamber is larger. For these reasons the floor of the orbits in the amphibians, in so far as it is formed by the palatine and ectopterygoid, together with the floor of the olfactory chamber (the prevomer) is displaced far backward and inward. A third and perhaps the most probable assumption is that, in addition to the backward displacement of the eyes and the enlargement of the olfactory chamber, there was also a marked decrease in the size of the semicircular canals, which in many primitive fishes are much larger than those of amphibians. The latter change would result in the occipital region's being displaced forward until it came to lie immediately behind the basipterygoid processes.

In conformity with the foregoing displacements the temporomandibular fossæ are now opened up, the pterygoids are beginning to be modeled in the direction of those of more typical tetrapods and the interpterygoid space is greatly restricted.

*Stage III. Primitive Permo-Carboniferous reptile, Seymouria*

Figure from Watson. Data from Broili, Williston, Watson, Romer.

This form is so primitive (for a reptile) that Sushkin and Broom prefer to remove

it altogether from the Class Reptilia. It was indeed a survivor of the earlier amphibians in the following features:

(1) In the arrangement of all the elements of the primary and secondary upper jaws;

(2) In the presence of separate ossicles (the "mesopterygoids" of Broom), lying between the basipterygoid processes of the basisphenoid and the pterygoids;

(3) In all the relations of the stapes, which, unlike that of reptiles, does not articulate with the quadrate (Sushkin);

(4) In the labyrinthodont character of the teeth (Broili);

(5) In the truncate form of the circular occipital condyle, which is broadly pierced by the notochord.

On the other hand, the whole norma basalis appears to afford a favorable starting-point for those of the higher tetrapods and both Watson and Romer argue that the amphibian connection of the stapes is not irreconcilable with primitive reptilian affiliations. The modelling of the pterygoids has proceeded in the direction of the reptiles and there is already a tendency for the anterior process to be narrow and for the descending processes to be developed.

*Stage IV. Captorhinus, advanced cotylosaurian reptile of the Permian*

Figure and data from specimen. Data also from Broom, von Huene, Sushkin.

Inspection of the figure will show that this form has retained many fundamental characters of its predecessors. On the other hand, the norma basalis has almost reached the stage formerly called the "rhynchocephalian palate," in recognition of the relatively primitive character of the palate of the existing *Sphenodon*. Probably the small size of the parasphenoid may carry this a little out of the direct line of ascent and toward the more typical reptiles, but on the whole it presents a very generalized reptilian stage structurally ancestral to that of the mammal-like reptiles. Thus, the pterygoids are already pinched in toward the midline; the occipital condyle is ball-like and the stapes is in contact laterally with the quadrate. The form of the forepart of the skull as a whole distinctly approaches that of the theromorph series.

*Stage V. Scylacops, primitive mammal-like reptile of the Middle Permian*

Figure and data from Broom.

At a superficial glance the norma basalis of this skull retains much that is characteristically reptilian; for instance, the anterior position of the internal nares, the strong development of the pterygoids, the unimpaired quadrates and the single ball-like occipital condyle. But a nearer view discloses a series of characters that prophecy the higher grades of this order and the advent of the mammals.

(1) There is a prophecy of the mammalian secondary palate. Dr. R. Broom informs me that on either side of the elongated internal narial opening there is a horizontal ridge on the maxilla and the palatine, which apparently marks the attachment of the fleshy palate, so that in life the inspired air was probably passed backward above this fleshy bridge to the opening in the U-shaped depression of the palatines.

(2) A notable advance toward the mammalian condition is seen in the marked reduction and slenderness of the posterior or quadrate ramus of the pterygoid.

(3) The squamosal has become conspicuous as the main brace of the zygomatic arch and together with the jugal is substantially in the primitive mammalian position at the posteroexternal corner of the skull.

(4) The opposite pterygoids have been pinched together along the midline, doubtless affording insertion to the strong pterygomandibular muscles.

(5) The keeled parasphenoid in the ventral aspect is beginning to assume the appearance of the mammalian vomer and Dr. Broom informs me that cross-sections of the skull of a typical gorgonopsian demonstrate the complete correspondence and homology of the parasphenoid with the mammalian vomer.

(6) The ectopterygoids are notably reduced in size and are approaching their final disappearance.

(7) The palatines are beginning to draw away from the front part of the skull and to take up their position in the middle of the palate.

(8) The dentition is differentiated into incisors, canines and cheek teeth.

(9) The stapes has precisely the same relations to the quadrate that its homologue in the mammals does with the incus, a point which will be more fully noticed below.

(10) The inner ear is displaced toward the ventral side of the skull.

*Stage VI. Cynidiognathus, advanced mammal-like reptile of the Triassic*

Figure from Broom. Data from Seeley, Haughton, Broom.

The norma basalis reveals a form that is evidently related to the gorgonopsians (Stage V) but which has advanced far beyond them in the direction of the Mammalia.

(1) The secondary bony palate, consisting of horizontal flanges from the maxillæ and the palatines, is complete and composed of the same elements as in the mammals.

(2) The pterygoids are diminished in importance, especially the quadrate ramus, which has been partly crowded out by

(3) The progressive development of the epipterygoid, which has assumed the characters of its homologue, the mammalian alisphenoid. This element has precisely the same position and nearly the same attachments as the mammalian alisphenoid and its homology with that element is extremely probable (See Gregory and Noble, 1924).

(4) The quadrate is now notably diminished and the quadratojugal slightly more so; so that a further continuation of the same tendency would reduce the quadrate to the size of the mammalian incus, with which there are many reasons to identify it.

(5) The zygomatic portion of the squamosal is substantially mammalian in all its essential relations.

(6) The temporo-mandibular fossæ have nearly assumed the mammalian character.

(7) The occipital condyle has become double and although the median portion is formed of the basioccipital, the exoccipitals contribute to the lateral portion (Broom).

(8) The stapes corresponds to the mammalian stapes in its connection with the inner ear on one side and with the quadrate (= incus) on the other.

(9) The ectopterygoid, as identified by Broom, is reduced.

(10) The dentition has attained the completely mammalian grade of differentiation into incisors, canines, premolars and molars. The adult dentition is preceded by a single set, representing the deciduous incisors, canines and premolars (Broom). Apparently the molars have no deciduous predecessors.

On the other hand, the vomer (parasphenoid) retains much of its primitive posterior position. That this bone is the homologue of the vomer is indicated by the fact that in *Dicynodon* the same element has an anterior process which

immediately underlies the presphenoid (Broom).

*Stage VII. Thylacinus, modern marsupial mammal, representing a survivor of Cretaceous marsupial stock*

Figure and data from specimens.

This modern form represents very well the essential architecture of the skull that was apparently characteristic of the Cretaceous polyprotodont marsupials. It is not in the direct line of ascent but is nevertheless typical on the whole of the primitive mammalian stage. The dentition of *Thylacinus* is of a relatively primitive mammalian type, the general pattern of the premolars and molars being inherited in basic features from the primitive placental mammals of the Cretaceous period.

Great advances beyond the cynodont stage are seen in the following characters:

(1) The completion of the mammalian secondary palate by the backward production of the palatine bar behind the level of the cheek teeth.

(2) The complete disappearance of the quadrate from the norma basalis and its retreat into the cavity of the middle ear.

(3) The completion of the modelling of the zygomatic portion of the squamosal for the support of the mandible, correlated with the development of a new or distinctly mammalian contact between the ascending ramus of the dentary and the glenoid region of the squamosal.

(4) The loss of the postorbital element, including the bar connecting the frontal and the jugal.

(5) Great diminution of the pterygoids, which are functionally replaced by the pterygoid flanges of the now dominant alisphenoids.

(6) Forward retreat of the vomer from the basisphenoid, exposing the latter in the ventral view.

(7) Development of a middle ear chamber or cavum tympani, in this case covered by a bony shell from the dominant alisphenoid.

(8) Withdrawal of the true otic elements from the plane of the base of the cranium; in this case they are largely covered by the alisphenoid bullæ.

(9) Completion of the paired occipital condyles.

*Stage VIII. Adapis, representing Eocene lemuroid primates*

Figure and data from Stehlin.

A great advance beyond the primitive mammalian condition is recorded in the norma basalis of this relatively early primate. Three leading factors have conditioned this advance, as follows:

(1) The elaboration of the upper molar teeth from the primitive tritubercular carnivorous to the quadritubercular frugivorous stage with incipient changes in the same direction in the posterior premolars. The incisors, now reduced in number to two on each side, have acquired more or less chisel-shaped crowns. The form of the canine is better adapted for frugivorous than carnivorous habits.

(2) The peculiar development of the dentition described above doubtless has conditioned the broadening of the jaw muscles and of the secondary palate, together with the shortening and broadening of the pterygoid region; the fossæ for the origin of the pterygoid muscles being conspicuously developed.

(3) The anteroposterior shortening of the jaws, correlated with the change from snapping and shearing to piercing and cutting, has caused the glenoid fossa to be displaced forward considerably in front of the basioccipital.

(4) A marked increase in the volume of the brain has conditioned the widening of the basicranial region.

(5) The chamber of the middle ear has become greatly enlarged and covered by the entotympanic, a bone of disputed origin but probably a neomorph derived from the extension of bony tissue around the inner side of the tubotympanal expansion. The true tympanic bone lies within this cavity covered by the entotympanic.

(6) Another indication of advance beyond the primitive mammalian stage is the beginning of the downward flexure of the basicranial axis upon the axis of the vertebral column, indicated by the partial exposure of the foramen magnum in the ventral aspect.

*Stage IX. Chimpanzee, representing a little-modified survivor of the Miocene anthropoid stock*

Figure and data from specimen.

A great advance in the direction of man has been achieved by this animal, which is indeed far nearer to man than it is to the primitive lemuroid of Stage VIII. The dominant factors in this advance have been the great increase in the volume of the brain, the marked downward flexure of the skull upon the column correlated with more or less erect position during locomotion in the trees. Again, in response to advanced frugivorous adaptations, the jaws and palate have been much shortened anteroposteriorly. The dental formula is reduced to that of man. The premaxillæ are fused with the maxillæ. The central chisel-like incisors are widened, perhaps for the cutting of fruit and tender shoots. The palatines have now completed their retreat to the posterior end of the palate. The pterygoids have shrunken into slender delicate slips of bone which are closely appressed to the descending flanges of the sphenoid. The retreat of the vomer toward the palate is also complete. The true tympanic bone has now escaped from its confinement within the cavity of the entotympanic and has fused with the expanded periotic, which forms the remnant of the ancient bulla.

The foramen magnum is widely exposed in the norma basalis and the mastoid portion of the periotic is expanded.

The temporo-mandibular fossæ are much shortened anteroposteriorly in correlation with the forward displacement of the squamosal and its glenoid cavity. The anterior part of the zygomatic arch forms a sharp elbow with the projecting process of the maxilla.

*Stage X. Homo sapiens, represented by aboriginal Australian, survivor of Pleistocene man*

Figure and data from specimen.

No more convincing evidence of man's derivation from a primitive anthropoid stock could be afforded than the fundamental resemblance of this skull in the norma basalis to that of the chimpanzee. At nearly all points it has advanced beyond the chimpanzee in the same direction in which the latter had progressed beyond the primitive Eocene primate. Thus there is a further shortening of the jaws, a further constriction of the temporo-mandibular fossæ, a further angulation of the maxillary with the jugal, a further forward displacement of the squamosal, a further backward expansion of the braincase, a further exposure of the foramen magnum, due to the more pronounced cranial flexure, and so forth.

Special human features are seen in the shrinking of the canine teeth and of the forepart of the palate, in the marked diminution of the bulla and its conjoined tympanic bone, also in the downward growth of the mastoid process.

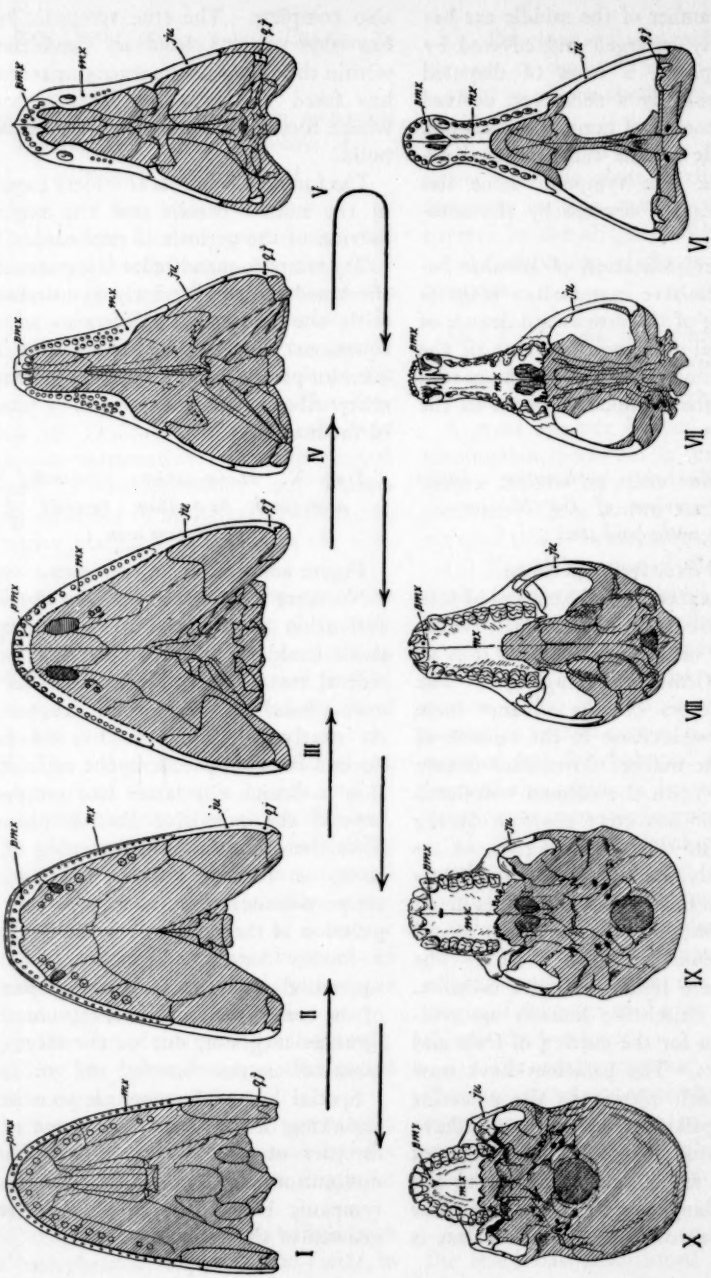


FIG. 2. EVOLUTION OF THE OUTER JAW SERIES

Same stages as in Fig. 1. White = *pmx, mx, ju, quj*. Cross-hatched = all the rest.

## HISTORY OF THE INDIVIDUAL ELEMENTS OF THE SKULL

### *I. Jaw elements*

*A. Outer, or secondary jaw.* In Stage I the dermal plates are far less differentiated from each other than in the final stage. Thus the premaxilla and the maxilla in norma basalis form narrow strips bearing small similar teeth forming part of the general bony mask of the face. The jugal and quadratojugal are in series with these elements. By the time we have reached Stage V, marked differentiation in this series has become apparent. In Stage VI the quadratojugal is reduced almost to vestigial proportions and the jugal has almost acquired its mammalian character. The premaxillæ and maxillæ both have secondary palatal plates. With the loss of the quadratojugal in the early mammals, together with the loss of the post-orbital bar, the conditions advanced toward the human stage. In Stage IX, represented by the chimpanzee, the premaxilla is fused with the maxilla in the adult, just as in man. The jugal is now limited to the front part of the zygomatic arch. In the final stage the contrast between the surviving elements of the secondary jaw series reaches its climax. The quadratojugal maintains its place in series with the secondary upper jaw and as an outer brace of the primary upper jaw throughout the first four stages, but becomes greatly reduced in Stages V and VI and disappears in mammals.

*B. Inner, or primary jaws.* The outstanding features of the history of this series of elements are:

(1) Steady diminution of the prevomers, which finally disappear from view early in the mammalian grade.

(2) Backward and inward displacement of the palatines, which are widely separated originally but finally meet in the midline (Stage V) and are found at the back part of the palate in Stages VI to X.

(3) Progressive reduction of the ectopterygoids, which are reduced almost to a vestigial condition in Stage VI and are absent in later stages.

(4) Modelling and extreme reduction of the pterygoids. In Stage I these are the dominant element of the primary upper jaw, widely separated in the midline. By Stage IV they have become highly differentiated, having no less than four main processes, not the least of which is the quadrate branch of the pterygoid. By Stage V this process begins to weaken. In Stage VI its place is largely usurped by the growing epipterygoid (alisphenoid). In mammals, Stages VII to X, the pterygoids are reduced to slips on the inner side of the descending flanges of the alisphenoid, where they are found in man.

(5) The quadrate maintains its primitive condition through the first four stages of the series, but in Stages V and VI its function as a supporting element is partly usurped by the progression of the zygomatic branch of the squamosal. In Stage VI the quadrate is a small element which however still retains its function as the suspensorium of the mandible. By Stage VII the quadrate has disappeared from view, being transformed into the minute incus of the middle ear.

### *II. Keel bone*

The vomer or parasphenoid always has a double relationship: on the one hand with the median septum of the nasal chamber and on the other hand with the roof of the mouth and the basisphenoid. In the mammals, including man, the vomer has lost its posterior extension over the basisphenoid and is found as a small element dividing the naso-pharyngeal tunnel in the midline.

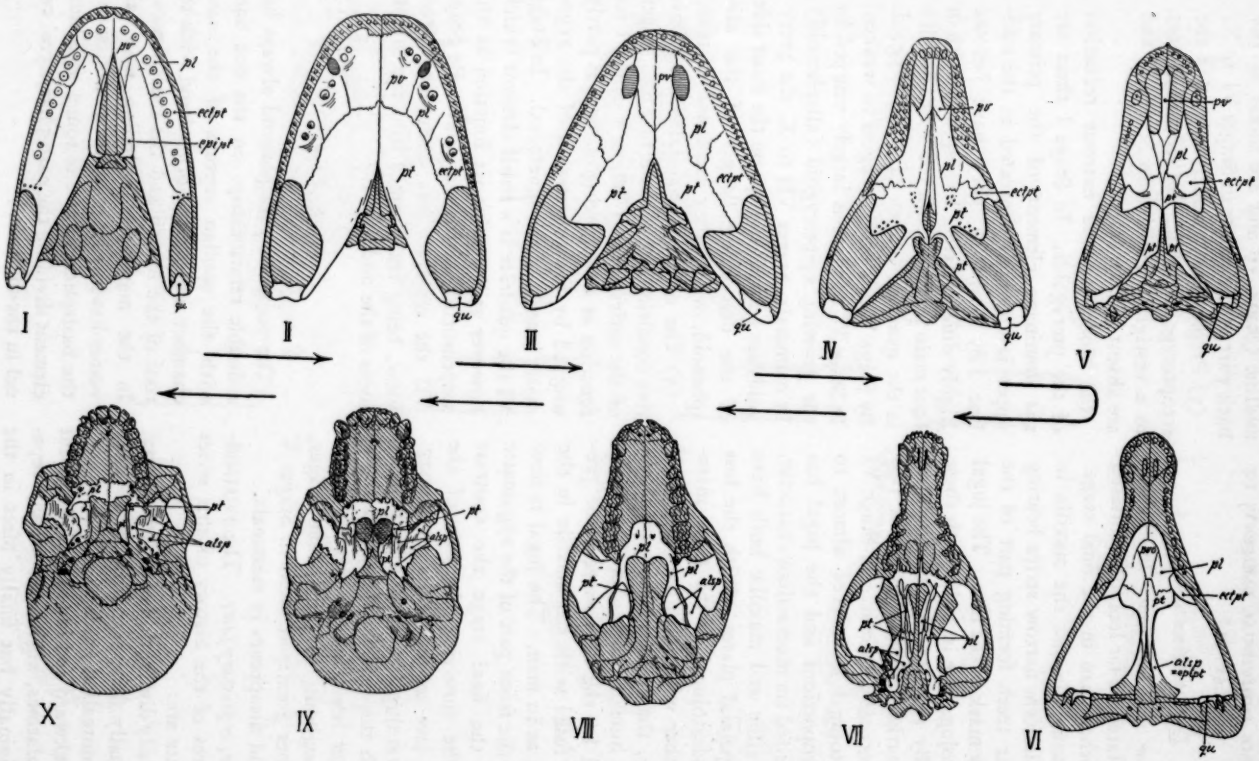


FIG. 3. EVOLUTION OF THE INNER JAW SERIES

Same stages as in Fig. 1. White = *pv*, *pl*, *ectpt*, *pt*, *epipt*. Cross-hatched = all the rest.

### *III. Basicranial elements*

The basisphenoid underlying the pituitary region of the brain in the early amphibians is covered by the parasphenoid but with the retreat of this element it is revealed as the central piece of the base of the cranium. In the early amphibians the basisphenoid sends out strong basipterygoid processes, which are covered by corresponding processes from the pterygoids. With the reduction of the pterygoids these processes lose their importance and disappear as we approach the mammals.

The basioccipital always constitutes the thrust-block between the vertebral column and the skull. In the lower vertebrates there is little movement between it and the column, but by Stage IV it has acquired a ball-like condyle which becomes subdivided into paired occipital condyles in Stage VI. These are at first located chiefly on the basioccipital but in the succeeding stages they shift apart laterally on to the exoccipitals.

### *IV. Temporal element*

The squamosal, a prominent element in the lateral view of the skull, does not appear in the norma basalis until Stage V, where it is beginning to constitute a new suspensorium of the mandible. This immensely important transformation is completed in the cynodonts and in the early mammals. With the great development of the braincase and the flexure of the skull upon the column, the glenoid portion of the squamosal is displaced relatively far forward in man.

### *V. Otocranial elements*

The otocranial region is largely developed in the norma basalis of Stage I. In the early tetrapod it forms the side walls of the braincase. By Stage V it has become partly displaced to the ventral side of the occipital region, where it is found in later stages. The sides of the brain trough are concealed from the basal view in all the earlier stages but in the primitive mammal skull, owing to the expansion of the neopallium, they begin to appear in the ventral view; in the chimpanzee and still more in man they become enormously developed.

### *VI. Hyobranchial elements*

The history of the middle ear bones from fish to man may be epitomized from the researches of Reichert, Gaupp and many other authorities, as follows: The stapes, or columella, of higher vertebrates is apparently represented in the fish by one of the hyoidean elements, either the hyomandibular, according to most authors, or the pharyngo-hyal, according to Woskoboinikoff, Schmalhausen and Sushkin. In the typical fishes the upper hyoidean segments serve for the support of the operculum of the gill chamber and of the hyoidean gill-arch. With the loss of the gills and operculum, the hyomandibula (or perhaps the pharyngo-hyal) is retained in contact with the tympanic membrane (which covers the "otic notch" in the position of the now obsolete bony operculum) and transmits to the inner ear the vibrations caused by sound waves impinging against the tympanum. In the mammal-like reptiles the outer end of the stapes was in contact with the quadrate or posterior element of the primary upper jaw, while the tympanic membrane was probably attached to the squamosal and to the back part of the articular bone of the lower jaw. Thus, as in recent reptiles, the back part of the jaw elements were probably already sharing in the vibrations of the tensely stretched drum membrane. By the time of the cynodonts the quadrate was a small element and the dentary was the dominant

part of the lower jaw; the stapes, at least in the smaller cynodonts, was perforated, presumably by the stapedial artery, exactly like the stapes of mammals. When the dentary grew upward and backward and established the new or mammalian joint between itself and the squamosal bone (see Part I of this article) the quadrate and articular bones were relieved of their functions as jaw elements while retaining and intensifying their functions in transmitting pulsations to the stapes and thence to the cochlea of the inner ear. Thus the curious auditory ossicles of man have been derived by change of function from the primary jaw elements and hyoidean arch of the fish. In this connection it is of interest to note that, according to Doran, the auditory ossicles of the gorilla and the chimpanzee closely resemble those of man. The ossicles in mammals become enclosed in a chamber which is a diverticulum of the tubotympanal canal and this in turn is encased in a bony shell, the auditory bulla.

## CONCLUSION

A survey of the series as a whole indicates that the bony tracts of the skull often appear to be moulded around or with reference to other structures which are frequently represented by fossæ in the dried skeleton. Thus the shape of the pterygoids is determined partly by their position between the temporo-mandibular muscles on the outer side and the pharynx on the inner side. Even in mammals, in which the pterygoids are greatly reduced, their shape is partly determined by their position in the bony wall of the pharynx. It is also evident that the form of a particular bone is partly determined by its position with reference to the midline of the skull as well as to the axis and direction of locomotion and the resulting orientation of the dorsal and ventral surfaces. Again, the shape of a bone is obviously in adjustment to the particular nature of the stresses (due to gravitation and muscular contraction) to which it is subjected, while on the other hand, its shape limits the movements and conditions the form of parts that impinge upon it, as in the basioccipital condyle. The presence or absence of a given bone in a particular type of skull, its general position and contacts are also obviously determined in part by its phylogenetic history in the stages preceding the present life habits. The increase or decrease of any given bone naturally tends to change the form of the skull as a whole. On the other hand, there appears to be some regulating mechanism, analogous with surface tension, which keeps the members of a functional series more or less in line, more so in the earlier and less differentiated stages than in the later ones. Compare, for example, the subordination of the premaxillæ, maxillæ and jugals to each other and to the parabolic contours of the jaws as a whole in Stages I, II, III, with the bold individuality of each of these elements in Stage VII; also with the later de-differentiation of the premaxillæ and maxillæ in Stages VIII, IX, X.

Whatever may be the complex causes, it is a fact that during a long geologic period a given element such as the ectopterygoid may gradually be relieved of its functions, or in other words, may be crowded out by a more aggressive neighbor. Thus we have the allied phenomena called the "change of function" and the "substitution of one part for the other."

While bones may be pushed apart, grooved or moulded, yet they naturally show a certain conservatism or inertia; otherwise the skull patterns would be so evanescent that we could never homologize elements through long reaches of

geological time. The persistence of the skull elements is illustrated by the retention of so many of them throughout the series from fish to man. In the norma basalis this is more marked than in the norma lateralis. Of the full complement of bones present in the fish represented in Stage I, the only ones not preserved in man are the prevomers, ectopterygoids, quadratojugals. Of the rest, the quadrate has been taken over into the middle ear and is hidden from view, the epipterygoid has probably become the great wing of the sphenoid, the parasphenoid has become the vomer, the proötic has probably fused with the opisthotic. All the rest are present although greatly changed in form.

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# POPULATIONS OF ANT MOUNDS

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THE social insects, ants, bees, termites, resemble man not only in the numbers living together but in the construction of dwellings so very much larger than the individuals that make them. The number of individuals employed in such constructions is one element of success; yet the number is small in man as compared with these social insects. We can easily count the men who construct or who dwell in either a communal house of the South Sea Islanders or a modern hotel or apartment house, but in the bee hive only laborious methods reveal the fact that the individuals are from ten thousand to seventy thousand in one dwelling, while in a certain dwelling of a termite in Jamaica we counted no less than 631,878 individuals. Of this population about nine-tenths were full grown workers.

Ants in an ant hill have for the most part escaped all exact census and it is our purpose to add something to the scanty knowledge of this aspect of these social animals. The common small ant hills may be but ephemeral byproducts of mining operations, but the large ant mounds constructed of earth both in Europe and in the United States may persist through many years as community houses for successive generations of family groups that build and inhabit them as homes.

In 1906, when K. Escherich wrote his book on the life of ants, he could only report that the most populous ant mounds were those of *Formica rufa*, *F. exsecta*, *F. pratensis*, and *F. exsectoides;* and that in Switzerland the leading student of ants, Forel, had estimated the numbers in a mound of *F. pratensis* to contain 100,000 ants, while Sir John Lubbock, first Lord Avebury, thought 400,000 to 500,000 to be a probable number but that Young had counted from 50,000 to 100,000 in *F. rufa*. That left it in doubt whether the populations of ant mounds are of the magnitude of the termite or the honey-bee populations; and this seems the present-day state of the question.

No data as to numbers are reported for American ants that make large mounds, though the pioneer in the study of these mounds where present in large numbers in Pennsylvania, the Rev. H. C. McCook, was so impressed by the great size of the mounds in comparison with the smallness of the builders that he calculated that man built the great pyramid sixty-nine million times his own bulk, but that the ant built its pyramid-like dwelling six thousand eight hundred million times the ant's bulk.

Here in Maryland this same ant, *Formica exsectoides* F., presents fine groups of mounds not only here and there in the mountains of Garrett County, and in the Blue Ridge, but also near Baltimore, in Baltimore County; and especially over a large area in Montgomery and in Prince George's counties, toward Washington, as made known by the State Entomologist, Dr. E. N. Cory.

HOW CAN WE ESTIMATE THE POPULATION OF AN ANT MOUND?

When first observing these very active insects swarming over the mound and over the food trees that may be one hundred feet distant from the mound, one's impression may be that the population is vast; however it is to be borne in mind that each ant, running at the rate of some fourteen feet a minute, may appear in many places in quick succession, and careful examination shows that the ants are not uniformly distributed all over the terrain but that they are running chiefly in certain paths that lead to their food trees.

By counting the ants on such paths we gain some notion of the actual population that is busy here. From an average sized mound, in five minutes, we noted eighty-three ants running out from the mound toward the tree that supplied food and as many more ants returning. As some ants marked with paint spent often about half an hour away from the mound, there were likely enough five hundred ants making use of this path at one time; and as most mounds have several paths there may well be a few thousands of ants thus out foraging in the territory outside the mound.

At the same time on the surface of the mound one may often see very many ants busy in the maintenance and growth of the mound; hurrying toward the apex, and more rapidly dashing down to the base after having deposited a stick, leaf, or stone for the building. To estimate the numbers of these ants on the mound we hold over them here and there a square wire frame six inches wide, and count the ants circumscribed for a moment by this quarter of a square foot area. The numbers range from eight to eighty on different mounds and upon different parts of the same mound.

An especially large mound calculated to present sixty-two feet of surface was found to be overrun with about sixty ants to the average square foot, as measured in many places, so that there one might see 3,720 ants working on this exceptionally large edifice, at one time.

That the numbers of ants working on a mound may be great is also suggested by the work accomplished; thus when two quarts of small stones, estimated as 56,135 individual pieces of crystalline limestone fragments, were placed at the base of a certain mound, it was found that in three days the ants had carried many pieces up and had scattered them rather uniformly (as is their wont, with building materials), over the surface of the mound with an average of 1,514 stones per square foot or a total of 19,051 stones. Since each stone is carried by only one ant at a time, and though the distance the stones were carried or dragged was less than two feet, one would suppose large numbers to have been at work. This is especially probable as, often, each stone is not carried all the way in one trip but laid down and later carried onwards by another ant, so that the number of portages was greater than the number of stones. However, each ant works very rapidly and for long times and a few hundred will accomplish an astonishing amount of work; yet in three days it is probable that successive sets of ants were engaged in the above task and this means many ants involved.

Besides the ants on the road and on the mound at times of construction there are many ants within the mound, as evidenced by breaking into it and finding many attending the young and in vigorous defense against attacks; while pieces of shingles placed on the mounds revealed in subsequent days large aggregates of ants collected under the shingles to rest in appreciation of the warmth afforded

through the insolation of these artificial roofs.

A more definite approach to a census of the population of the mound comes from the observation that in September some mounds are thickly strewn, as with handfuls of wheat, with the cast-off pupa cases or swaddling clothes of the young, brought out by the ants from the interior and strewn as building materials over the mound surface. Each of these represents a new ant added to the population. Counts of these empty cases by the above wire frame gave an average of 212 per square foot or a total of 13,144 for the very large mound. But two days later rain, wind and the accumulation of other building materials had reduced the visible pupa cases to 7,000. Another mound also showed pupa cases at the rate of 200 to the square foot and had this mound the size of the other there would have been 12,400 ants represented.

Thus in the mound, on the mound, and in the neighborhood of the mound, there are thousands of ants that use the mound as their place of origin, to which they return to care for and feed the young. But as many ants work all night in the warmer season there is no time when all the ants can be taken within the dwelling, hence a complete census is difficult.

### ANT MIGRATIONS

On rare occasions most of the ants combine in a common hegira, flowing out over the earth to found a new mound and leaving the old one more or less depopulated. This suggests the possibility of counting the population as it migrates. On one occasion for twelve days in July 1926 the ants of a large mound were thus migrating out to a new mound, all in one path from four feet wide to later two feet wide, dwindling as the days went by. This run of ants out of the old mound lasted the greater part of the day time and at any one minute there were as many as forty ants leaving; yet about as many returned, since the ants run in both directions. However, many of these going out carried each a burden, either a full grown worker or else one of the young ants, while few of those returning carried ants. If we could have counted the numbers of ants carried out in excess of those carried back, we might have calculated the entire number of ants taken to the new mound.

With our very imperfect data it seemed only that some thousands of ants were concerned in this migration. But at the speed of running, one ant might cover the forty-five feet from the old to the new mound and return to be counted again every twenty minutes, so that a few hundred ants might have done the chief portage of the carried ants, had they lost no time. In this case no complete census of the old mound was possible, since not all the ants left it permanently but both mounds continued to flourish as populous communities.

Forel, however, was able to base his estimates of the numbers of ants in an average mound of *F. pratensis*, in Switzerland, upon such a migration, which he watched from its incidence onward at times each day for an equivalent of eight days of good weather. Every day the march began at half after nine and lasted about seven hours, stopping rather sharply with the oncoming of the cool nights in May. The ants remained in the old or in the new mound till the following morning, when those in the old mound started the trek again before any ants had come back from the new mound. Forel saw an average of thirty-four adult worker ants carried bodily away from the old mound each minute and on this basis he calculated the entire numbers thus

transported to the new mound as 114,000; but, to allow for sources of error in the data, he supposed the sum to have been from 50,000 to 150,000.

Forel then judged that from this average mound having a population of one hundred thousand ants more or less, it might be inferred that a small mound would contain from five to ten thousand ants but that very large mounds might harbor 400,000 to 500,000 adult ants.

These last suppositions were accepted by Sir John Lubbock, who states (10, page 119) that ant mounds are more populous than bee hives and that in larger communities of *F. pratensis* "it is possible there may be as many as 400,000 to 500,000 ants and in other cases even these large numbers are exceeded."

A possible criticism of all estimates of populations based upon actual migrations is that there is no proof that ants carried to a new mound one day may not return another day and themselves act as porters or even themselves be carried several times, which would lessen the calculated population.

### TAKING AN ANT CENSUS

A much surer basis for counting the community seemed to be found in the fact that all the ants of a mound retire into a torpid condition within and under the mound every winter and then should be all obtainable in a concentrated space. With this in mind, a certain average sized mound nineteen inches in height, fifteen feet in circumference, and five feet over the top, in Montgomery County, was dug up February 12, 1928. Some description of this region and of the mound-structure may then elucidate the conditions of census-taking by this method.

With small scattered oak and pine trees the thin layer of dark humus full of matted roots of huckleberry, etc., overlies a sticky, light colored clay full of pebbles. Erupting from the subsoil through the humus the mound had spread laterally as a conical mass of gray earth commingled with bits of vegetable matter and such minute pebbles as the ants had collected.

The firm roof of the mound, one to three centimeters thick, was perforated, near the base only, by entrances into the internal labyrinth of passageways running somewhat parallel to the outer surface, but interconnected in different layers by many radial passageways, the whole forming a dense network branching every 40 mm. or so. The network was more dense near the surface, especially that to the south and from it there extended downward beneath the mound some twenty shafts with various side drifts; shafts being seven by seven and others nine by nine millimeters in diameter. Almost all the short passageways of the labyrinth net were wider than deep; of thirty-three measured, only six had equal diameters and twenty-seven ranged from 19 by 9 to 8 by 6 with average of 12–4 by 9. In all these tunnels the roof was markedly different from the floor; the roof or ceiling was rough and with projections of earth and stone as if roughly bitten out, while the floor was smooth as if much trodden when moist.

To obtain the ants a ditch was dug close to the south edge of the mound down to water at two feet depth; the mound was carefully shovelled out and the ants captured by spooning them out from the vertical tunnels, side drifts and the lower labyrinths, in which the ants were found matted together in dense dark masses with intermingled legs; they occurred in separate tunnels as much as two feet apart and not at all in one common bed.

These ants were in the semitorpid state

in which the similar ant *Formica ulkei* was found by Holmquist; all were capable of slow locomotion at temperatures of five and even three degrees C., 20 to 24 inches down in the earth and showed their main responses, climbing and biting at the glass thermometer or seizing hold of bits of cloth and being thus captured; or in some cases carrying mouthfuls of earth, as if to repair the damage done to the mound.

Though the temperature of the air was 5°C., that within the soil only 3°C., and though the thermometer on the north face of the mound, in the sunshine, registered but 4.5° and within the upper part near the stump only zero with fine crystals of ice in the passageways of the labyrinth; yet in the labyrinth of the south part of the mound there was a temperature of 8°, owing to that storing up of sun heat so carefully investigated by Steiner in the mounds of *F. rufa* and observed in *F. exsectoides* by Andrews. It was here that some few ants first emerged, having not yet retired with the majority to the lower levels beneath the mound. Presumably, as in *F. ulkei*, these upper ants may be those that work on the mound top to the last moment long after the main population had gone into semihibernation below.

Yet the most active ants were by no means as active as in summer, and in bottles they gave off little or no odor of formic acid. With the very high water table, some of the ants seemed to be hibernating below water level, since in digging the deeper tunnels water gushed out carrying ants floating upon it, sluiced out by change in pressure conditions and here again it is possible, as suggested by Holmquist, that the ants may hold air in the tunnels even below water level.

The ants collected in jars and cans, alive or dead, were counted at 5°C. on February 13–17, as 4,802 living and 1,005 dead workers with ten living queens, or perfect females, only one of which was injured.

As three people in several hours had failed to dig out all the mound, some of the earth was replaced and left till May 6, in the hope that the remaining population could be captured with less mortality when not deep down in the gravel and clay, even though more active then.

At this date, the temperatures being 17–19°C., the ants were active on the mounds, food trees, and paths getting food from aphids and certain scale insects on scrub pine trees and apparently drinking from injured unfolding leaves. The ruins of the dug out mound were already worked over by the part of the population not removed in February; about an inch deep of pellets had been assembled over the surface of the mound rising above the old stump and here some two hundred ants were now at work. Only a few ants were discovered passing out from this mound to small oak trees some fifteen feet west and east of the mound, and on these very few ants could be found. Two of these were drinking juice from an injured shoot, with unfolding leaves about two inches in length, and it seemed that this juice arose from injuries in the stem caused by insect larvae. Though a dozen or twenty of these ants were busy struggling to bring home a small millipede on the ground, it did not appear that this population had as yet any well established source of food, even though it had done so much work in reconditioning the mound.

To collect these active ants they were stimulated by drawing bits of rag slowly over the mound and then when the pugnacious ants had seized or mounted upon the rags they were thrown into a large milk can or else the ants were shaken off into it. After removal of all ants on the surface, the mound was dug into and

the ants removed in the same way, as they swarmed out of the labyrinths that they had constructed since February. These ants occurred scattered here and there, and some deep down in the wet gravel in one mass of twenty or more were still jammed close together as in winter rest, having apparently never been awakened as yet by the outer temperatures. Though the weather had been very hot the temperature where these ants were hibernating was but 14°C. These ants were sluggish, those above were active but not so much so as in summer. This is in close agreement with the findings of Holmquist that in *F. ulkei* Emory, some ants lingered on in hibernation up to May 14.

All the ants collected in four hours by three people were counted May 9 and 10 with the expedient of lowering a glass rod into the container in which the ants were active and then removing it when a few had responded to this attack by mounting upon and seizing the rod; these five to ten were counted and brushed off with the fingers into a receptacle. The few remaining dead ants were dumped out and counted individually. The living were 2,322 and the one queen and the dead were only 99, making 2,422 to be added to the part of the population collected in February. This made a total ant population of 8,239, of which 11 were queens, and 8,228 workers; 7,135 being counted alive and 1,104 when dead.

Doubtless this census was not entirely complete, since several hundreds may have perished in the wet clay in February and some few may have been out on foraging parties in May, while even this second digging could not have discovered quite all the population. Hence the dug out mound was visited again on November 18, 1928, when on account of the exceptional warmth, with temperatures of 26° in the air and 20° within the mounds, and 33° on the apex in the sunshine, ants were still working on the mounds in that region. Yet the remainder of the dug out mound showed no life, the temperature within it was but 17°; digging revealed no ants. There were, however, evident signs that ants had done considerable work in reconstructing labyrinths in two distinct piles of earth thrown out in former diggings; but the washed condition of the surface, as well as the presence of open holes, showed that the ants had not carried on the usual fall completion of the mound as had other populations, and we inferred that the few ants that had been left from the digging in May had finally disappeared, possibly from old age, and from lack of a queen.

The counts from these three successive visits thus assign to the community when it went into winter quarters in the fall of 1927 a population of 8,239 plus whatever ants escaped counting, from death in the digging or from other causes, or escaped at the time of the May census.

It may be a conservative surmise that the entire population was ten thousand adult ants in this average domicile of *Formica exsectoides*. Thus far there are no data to show that this ant has ever such vast populations as those estimated by Forel and accepted by Lubbock for similar ant mounds in Europe. That these latter estimates were excessive seems evident from the results got by more precise methods in Switzerland by Emile Young, who, in 1897 and 1899, made for the ant *Formica rufa* the most satisfactory determinations of populations as yet available.

### YOUNG'S OBSERVATIONS

The mounds he studied were all similar to the ones we studied, having about the same base but steeper slopes and greater height; so that the largest had three times the volume of ours. His first method was

to count all the ants to be found in a certain populous mound, 60 cm. high and 114 cm. in width, after killing them in a half hour's exposure to carbon disulphide poured into the mound. This gave a total of 22,580 adult and 13,500 young ants of various ages; 36,080 in all; however, some escaped at the onset, some were away from the mound, and others were not found in the miserable week of labor to pick out the dead ants from the 80 kilos of earth carried off for minute study.

His second method was to visit populous mounds every day, preferably about 11 to 12 A.M. and to collect all the ants that appeared upon the surface of the mound with the aid of a little stick of one centimeter diameter which the ants attacked and mounted till he brushed them off into alcohol, making with seventy-five trials averaging 122 per trial, 9,203 ants in an hour; the next day 9,647, and so on for a week; but by that time the population was so much reduced that the remainder were to be sought by digging into the mound. In some cases, however, it was nearly a month before the population of the mound was exhausted.

Supplementing these domiciliary visits the author also collected the ants found seeking food upon trees and also those ants that were resting in temporary roadside shelters between the nest and the food trees. The author selected isolated ant hills, not any that were connected to perhaps a dozen others with common use of mounds; and he also noted that sometimes the ants disturbed by the census operations may move off in a body as much as 20 metres to some new mound. In such a manner Young obtained a census for no less than five mounds in diverse regions; in size ranging from 45 to 70 centimeters in height and from 95 to 160 centimeters in diameters.

The actual counts of adult working inhabitants of these five mounds were as follows: 19,933; 47,828; 53,018; 67,470; and 93,694. These census figures he regarded as only a beginning, which, he trusts, someone else may continue. Since ants always escaped the census he thinks that the addition of say 10,000 to each of the above would express the real population.

Young emphasizes the wide differences found in mounds of the same ant, one having a population nearly five times that of another. Moreover, there was no correlation between the size of the mound and the numbers of inhabitants. The smallest of these mounds had more than double the population of a much larger mound. The largest mound had scarcely more than half the population of the next to the smallest mound. Young suggested as probable that the smallest population found in a big mound may have been adversely influenced by the mound standing in shade almost all the day and having only two paths to food, in place of seven for the most populous mound.

It being thus shown by Young that these European ants *F. rufa* may inhabit domiciles crowded with from thirty to one hundred thousand adults and that, in one case at least, the young were about half as numerous as the adult workers, and that the numbers could not be inferred from the sizes of the mounds, it remained to be found out how far these numbers hold true for such American ants as *Formica exsectoides* F.

### LONGEVITY, NATALITY, AND MORTALITY IN ANTS

The smaller numbers we derived for the American ant might be due in part to the count being at the time of year when there were no young, while the summer counts in Europe allowed for newly

arrived adults being reckoned in, for these populations may well rise and fall through a single year according as successful breeding adds to the adult population or as poor conditions lead to rapid loss of adults. This raises the problems of length of life, birth rate, and mortality in these ants.

Unfortunately not much is known about these aspects of ant life. Lord Avebury states that worker ants had been kept by him from 1875 as late as 1881; but this possibility of longevity, great for insects, must be discounted for such large, wandering and very audacious ants as *Formica exsectoides*, exposed to all the risks of free life day and night and moreover working in the summer season at a rate that may be expected to be inimical to long life.

Attempts to keep *Formica exsectoides* in captivity and to make permanent mounds in new localities by frequent transportations of populations and additions of new workers led us to the conclusion that mortality may be great and that conditions of life may be such that communities rather rapidly become depopulated.

Observation of individual mounds through years in the best natural environment shows that some mounds become depopulated and may be deserted, while others increase in population, and yet other mounds hold their own for many years with very little apparent change.

Obviously, to maintain the community, the birthrate should at least be as great as the mortality. The mound serves for the protection of the few perfect females or so-called queens, which are the chief maintainers of the birthrate for the entire community, since the workers for the most part are not directly involved in reproduction.

The number of queens in a domicile is a determining factor in the problem of populations, and one of the most important elements in the maintenance and increase of the population of a mound must be the number of queens added to it. In our mound with 8,228 workers were found but eleven queens, but in another mound very little larger, we found as many as thirty-three queens and very large and populous mounds may be expected to contain even more.

The one queen of the above eleven, taken in May, began to lay in captivity at that season and produced a dozen eggs within three days. In this same species Pierson found that the queens continued breeding throughout the warm season in captivity. In *F. ulkei* the breeding season is only about one month according to Holmquist, who found that in captivity nine queens laid on the average 100 eggs in that season or some three eggs a day as compared with our ant that started at the rate of four eggs a day; even here, however, there is the added variable that one queen laid as many as 190 eggs or nearly twice the average of the nine.

Pierson also found in *Formica exsectoides* that the eggs became mature ants in about one month. If we assign a breeding season of three months with three broods, our eleven queens might add 1,320 adults per month; thus if these did not get killed, there might be some 3,960 new ants in the fall to go into winter quarters. On such basis half of the ants we counted in the winter might have been young ants born in the previous summer. This rate of birth might be offset by a corresponding mortality or it might lead to very rapid increase in the population through years as conditions warranted.

That the yearly increase may be proportionally very great and the mortality very large may also be inferred from the fact that Young counted in *F. rubra* 13,500 young with 36,080 adults, but as all the adults were not then in the mound, the

ratio of young and old was doubtless more nearly one to three than one to two.

On the other hand, Eidman, as quoted by Myers, kept in captivity the small ant *Lassius niger* and counted 3,456 adults with 11,600 young; that is, the young nearly three times the adults; but the ratio of one to three derived from *F. rufa* by Young is doubtless more nearly the truth for *F. exsectoides*, since these ants have so much the same habits and structure.

Our large mound showing some 13,144 young might then have had two to three times as many adults, or from 26 to 39 thousand ants, and were there no mortality the whole population to go into winter quarters might have been as great as forty to fifty thousand ants in place of the ten thousand ants more definitely determined for an average mound.

Since the average mound was very roughly not much over half the dimensions of the very large mound, it might have been expected to have but half the population; except for the important fact that Young found in *F. rufa* no correlation between the size of the mound and the populations; and but for the consideration that the mounds have areas and cubic capacities twice and four times the linear dimensions. Of these two factors, area and capacity, the former is the determining one for the population, since in large mounds the centers are no longer inhabited, while the surface is the real essence of the mound as supplying the sun heat essential for the well-being of the adults and for rearing young populations. We might then have assumed that the big mound should contain four times the population of the average mound of half the height; or forty thousand ants as survivors in winter.

In conclusion, there seems no convincing evidence that the populations of ants in American mounds here in the East are anything like what has been sometimes assumed; being of the order of ten to fifty thousand while the more exact estimates of Young for *Formica rufa* in Switzerland show thirty to one hundred thousand or more as probable.

With the sparse data at hand and considering the great numbers of unknown factors it would seem rash to assume that one of the specific differences between *F. rufa and F. exsectoides* lies in the size of populations, but that might prove to be the case with adequate data. In both cases the populations doubtless rise and fall annually somewhat as in the honey bee and their numbers are comparable with those of the honey bee; while on the other hand there is no reason to assume that these mound builders have such large numbers as half a million, as assumed by Forel and by Avebury, which would make these ant populations approach those of certain termites.

The size of the populations of these large ant mounds has some definite bearing upon the practical problem that these ants are accused of injury to forests: first by aiding the insects that suck juices of trees and secondly by actually killing some small trees near their mounds.

The mounds often occur in settlements, or colonies of few to many. In Baltimore county there is such a colony of some two hundred mounds and in the combined areas of Montgomery and Prince George's counties "infected" we counted 989 of which 127 were then occupied and in Pennsylvania there were at one time 1,600 mounds in one area and 1,800 in another colony, as stated by McCook. With such large numbers of mounds it becomes of importance to know whether the populations in one mound rise to the ten thousand, one hundred thousand, or the half million level.

With an estimated average of some ten

thousand ants in one mound, the Baltimore county colony may present about two million ants and that larger colony nearer Washington some eight million of ants. The statements in literature that such colonies contained hundreds of millions of ants seem to lack present basis of actual counts. Only the taking of an actual census of the ants in many mounds will eventually decide the question as to the average populations existent in these mounds.

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# NEW BIOLOGICAL BOOKS

*The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that* THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

## BRIEF NOTICES

### EVOLUTION

THE GREAT LIFE CYCLE.
*By William Irvin Utterback. The author* 10 cents *Huntington, West Virginia* $3\frac{3}{4}$ x $9\frac{1}{4}$; 2 pp.

It is high time that THE QUARTERLY REVIEW OF BIOLOGY gladdened the hearts of its readers once more with another contribution to its *Fundamentalist Portrait Gallery*. No more worthy candidate for this high honor could possibly be found than William Irvin Utterback, B.S., A.M., head of the department of zoology of Marshall College, Huntington, West Virginia, and author of "The Naiades of Missouri," "The Myth of the Manitou," "Biology and Human Welfare," etc., etc. The individuals who have been included in this series of *Portraits* hitherto have come from various walks of life, chiefly clerical, but we have not before had a professional zoologist, head of the department in a college of around 1500 students, of whom nearly 600 "are enrolled in biologic courses." We emphasize these technical points because they have an important relation to what follows, and because other professional biologists have some time been urging the editors of this REVIEW to give due attention to Professor Utterback's case.

The essence of Professor Utterback's contribution to the problem of organic evolution is exhibited in the full page chart, which is here reproduced with the permission of its author. We recommend its careful perusal. It demonstrates, with devastating clarity, the intellectual level to which the philosophy of reconciliation between science and theology belongs. In embracing this philosophy Professor Utterback does not stand alone. On the contrary he has not a few distinguished associates among professional scientific men, who, along with him, hold that science and theology can, and should be, reconciled. It is desirable for these gentlemen to see precisely the kind of thing this philosophy may lead to, and must lead to if followed through with any degree of thoroughness or persistence.

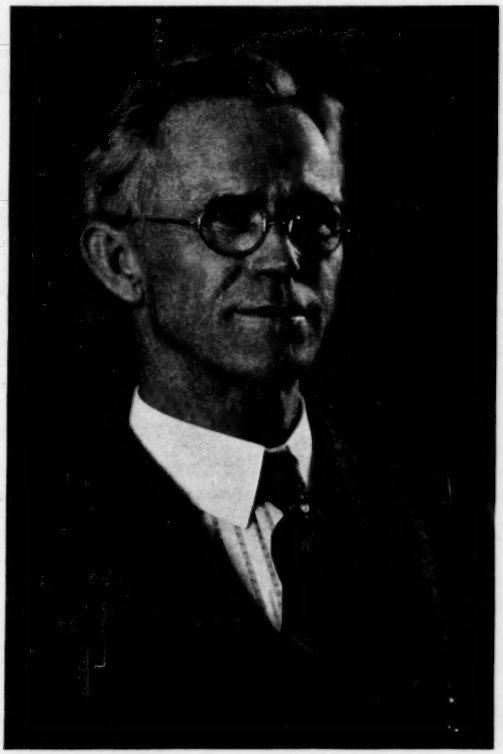
Coming now to Professor Utterback's text accompanying the chart we may first note what he says regarding its provenience.

No key is necessary in the use of this chart since the arrangement is intended to be self-explanatory if

the reader will start with "FIRE" as the point of construction and will follow the circle clock-wise until he ends with "FIRE" as that of destruction.

Through his many years of scientific and scriptural research the author has endeavored to harmonize the infallible scriptures with true science and also has attempted to project some light into the night of doubt relating to the evolution of man by making some discoveries concerning the origin and the early history of man. Some have said that science has a tendency to weaken our faith in the word and works of Deity, but the author of this chart has had a constant assurance of his faith while spending many years as professor of biology in both denominational and secular colleges. On one occasion the Presbyterian Synod of the State of Missouri honored him by sending him to organize a secondary college in the scene of Harold Bell Wright's famous novel, "The Shepherd of the Hills."

While presenting this controversial subject of organic evolution through newspaper, science journal, lecture room and even the pulpit and Bible class, the author has never been censured as a radical liberalist; however, his compromising views with the leading scientists, theologians and historians in regard to man's origin and destiny should not place him in the very same category with the extreme fundamentalists, yet his leaning may be more in that direction since it is his firm conviction that there is surely nothing to hinder a good biologist from tacking his faith to the supernatural as well as the natural.

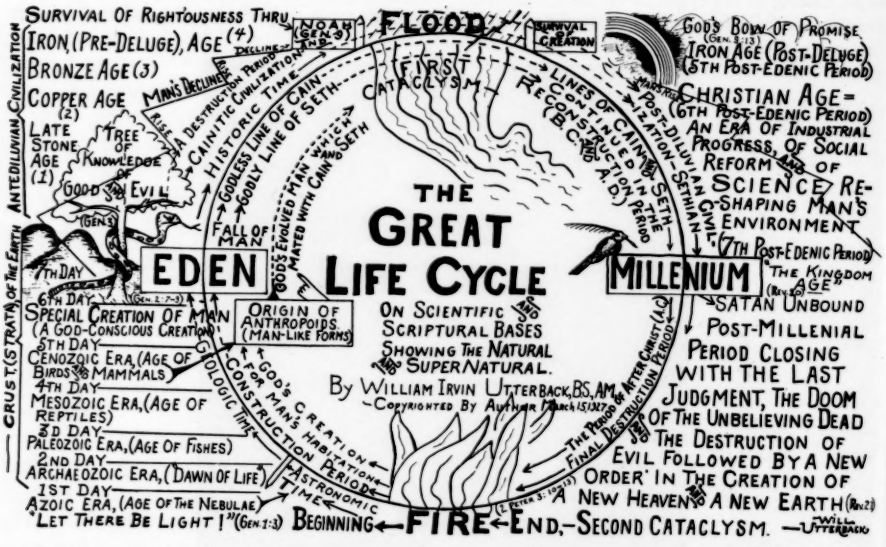


WILLIAM IRVIN UTTERBACK

The accompanying scheme is fashioned on such basis and is considered convincing by the dean of a foremost Divinity school and institute of sacred literature. Therefore, since this viewpoint on evolution also receives the endorsement of scientists and historians, the writer would dedicate it to God and man in acknowledgment of that divine and human love which will usher in a greater day.

The author identifies the fifth day of creation with the Cenozoic Era, and states that mammals, including anthropoids and *Pithecanthropus erectus*, were then brought into being.

Then came the Sixth and Final great Day in God's creation,—that wonderful era, the spirit of which still pervades our modern life. Now that the world was created for Man, a God-conscious man was finally created for the world. This was a super-man created directly by the hand of God in his own image in the


THE GREAT LIFE CYCLE
ON SCIENTIFIC AND SCRIPTURAL BASES SHOWING THE NATURAL AND SUPER-NATURAL.
By William Irvin Utterback, B.S., A.M.
—Copyrighted By Author March 15, 1927
EDEN
MILLENIUM
FLOOD
FIRST CATACLYSM
FIRE
SECOND CATACLYSM
SURVIVAL OF RIGHTOUSNESS THRU
IRON, (PRE-DELUGE), AGE (4)
BRONZE AGE (3)
COPPER AGE (2)
LATE STONE AGE (1)
TREE OF KNOWLEDGE OF GOOD & EVIL (GEN.)
FALL OF MAN
7TH DAY
6TH DAY
SPECIAL CREATION OF MAN (A GOD-CONSCIOUS CREATION)
5TH DAY
CENOZOIC ERA, (AGE OF BIRDS & MAMMALS)
4TH DAY
MESOZOIC ERA, (AGE OF REPTILES)
3D DAY
PALEOZOIC ERA, (AGE OF FISHES)
2ND DAY
ARCHAEOZOIC ERA, ("DAWN OF LIFE")
1ST DAY
AZOIC ERA, (AGE OF THE NEBULAE)
"LET THERE BE LIGHT!" (GEN. 1:3)
BEGINNING
END
ORIGIN OF ANTHROPOIDS (MAN-LIKE FORMS)
GEOLOGIC TIME
ASTRONOMIC TIME
GOD'S CREATION FOR MAN'S HABITATION CONSTRUCTION PERIODS
CRUST (STRATA) OF THE EARTH
ANTEDILUVIAN CIVILIZATION
MAN'S DECLINE
A DESTRUCTION PERIOD
CAINITIC CIVILIZATION
HISTORIC TIME
GODLESS LINE OF CAIN
GODLY LINE OF SETH
EVOLVED MAN MATED WITH CAIN
GOD'S MAN MATED WITH CAIN
NOAH (GEN. 5-9)
SURVIVAL & CREATION
LINES OF CAIN & SETH CONTINUED IN THE POST-DILUVIAN CIVILIZATION
RECONSTRUCTION PERIOD
GOD'S BOW OF PROMISE (GEN. 8:13)
IRON AGE (POST-DELUGE) (5TH POST-EDENIC PERIOD)
CHRISTIAN AGE = (6TH POST-EDENIC PERIOD) AN ERA OF INDUSTRIAL PROGRESS, OF SOCIAL REFORM AND OF SCIENCE RE-SHAPING MAN'S ENVIRONMENT
(7TH POST-EDENIC PERIOD) "THE KINGDOM AGE" (REV. 20)
SATAN UNBOUND
POST-MILLENIAL PERIOD CLOSING WITH THE LAST JUDGMENT, THE DOOM OF THE UNBELIEVING DEAD
THE DESTRUCTION OF EVIL FOLLOWED BY A NEW ORDER IN THE CREATION OF A NEW HEAVEN & A NEW EARTH (REV. 21)
—WILL UTTERBACK
THE PERIOD OF AFTER CHRIST (A.C.)
FINAL DESTRUCTION PERIOD
THE PERIOD OF BEFORE CHRIST (B.C.)
(2 PETER 3: 10-13)

THE Accompanying Chart is An Attempt To Show The Past, Present & Future No Key is necessary For its use Since The Arrangement is intended To be Self-Explanatory If the Reader will start with "FIRE" as the Point of Construction & will Follow the Circle Clock-wise until He Closes with "FIRE" as the Point of Destruction.

* * * * *

The Geologic, Historic & Future Periods of Time are Presented within this GREAT LIFE CYCLE As mostly Determined on the Scriptural & Scientific Bases As well As on Facts Gained Through The NATURAL & The SUPER-NATURAL

* * * * *

The Essential Features of this Presentation are That of the Mating of GOD'S Specially Created Man With His Evolved Human Form Followed By the Cainitic & Sethian Civilizations.

* * * * *

The Mingling of the God-Conscious with the Evolved Man Solves That Age-Old Problem of "Who were The Wives Of Cain & Seth? Without Encroachment Upon Orthodoxy

**All Forms Of Life Are Cycles**

The Above Illustrated Conception Is An Attempt To Compromise Modern Views Of The Scientist, Theologian And Historian. In This Grand Race Course The Great Eras of Fire is the Goal for Jehovah-the Creator, and Satan-the Destroyer. Four Parallels Are Seen Here in the Cataclysms of Fire and Flood, and in the Peaceful Periods of Eden and the Millenium. All Bounding Four Long Eras Alternating in Their Construction And Destruction.

As to the Time Element Covered By This Great Scheme the Divisions Are Compromised Estimates of Great Scholars may indicate Ten Billion Years Ago For Astronomic Time, One Billion Years For The Geologic Time, Ten Thousand For Historic Time; And, Judging From the Known Past, Twenty-Five Thousand Years For Future Time

* * * * *

According to most Commentators The "DAYS" of the Genesis Cosmogeny Are The Geologic Ages Whose Pages Are Plainly Read in God's other great Text, His Wonderful Earth-Book.

The Finite Mind of man is unable to fathom the Extent of the First Great Day when our Earth may Have Functioned As a Luminary in the Universe.

The Present Highly Heated Interior of the Earth is Positive Proof That the First Creation was Conceived in Fire By the Great Creator who Espoused the Cause of Self-Existent Righteousness with all its Attributes; however, Fire was made Destructive in the Hands of Satan who Championed the Cause of Self-Existent Sin with its Attending Attributes.

Yet God-Almighty Is The Greater Power!

* * * * *

Satan's Power May Have Prevailed In The Pre-Deluge Periods Of the Late Stone, Copper, Bronze & Iron Ages of the Post-Edenic Time, But God's Power was, is & Will Be, Dominant Throughout The Iron Age (Post-Deluge) & Christian Era Of Pre-Millenial Time.

* * * * *

The Crowning Age of Love & Peace,—The Great Millenium,—will Stand in the Same Constructive Relation As Eden Did to Its Six Geologic Ages. Since It will Come At the Close Of Six Historic Ages.

Symbolically Another Week Of Six Labor Days Shall Have Been Closed With the Seventh Day, (Millenium), as the Rest Day—An Age When Love will Predominate

* * * * *

Then will Come the Post-Christian Age, When, As in All Life Cycles, The Great Decline Will Begin Where The Most Productive Life Ends & After A Long, Final Conflict with Evil There will Come The Day of Jehovah-God when the Great Alpha & Omega,—The Beginning & The End,—Will Be Given The Victory in That the Elements will Melt With Fervent Heat Followed By A Reign of Righteousness without its Sting of Death Throughout Another GREAT LIFE CYCLE.

midst of perfect conditions,—a Paradise, or Eden. Here at last the great Creator had succeeded in establishing an innocent triune Man upon the earth where, at first, effective bars were erected against the destructive force of Satan.

The remainder of the story of human evolution runs as follows, according to Professor Utterback:

Just as fire was the beginning and will be the end of one Great Life Cycle, or Phylogeny, so in the dust of the earth is the beginning and the end of the individual, or Ontogeny, of man. The earth was cursed for man's sake since it is better for fallen men to struggle with the stubborn earth than to live without toil and thus the great pronouncement was made: "In the sweat of thy face thou shalt eat bread, till thou return unto the ground; for out of it wast thou taken; for dust thou art and to dust shalt thou return." However—

"Dust thou art to dust returnest
Was not spoken of the soul."

Yet the first representatives of God-conscious man, after yielding to the general sin of disobedience in tasting of "the tree of knowledge of Good and Evil," fell toward the level of those anthropoids who had dwelt outside of Eden and had now evolved to a primitive form of the genus Homo, represented by the highest types of Neanderthal Man, (*Homo Neanderthalensis*), and even by the Cro-Magnon type, the earliest form of Modern Man, (*Homo sapiens*). Outside of Paradise, at the time of the expulsion, the world was doubtless passing through a transitional period from the old stone age (Paleolithic) to the late stone age (Neolithic) which marks the beginning of modern man.

According to writers who are neither extreme fundamentalists, nor radical liberalists, the Genesis cosmogony is not in conflict with that of science and these same theologians who accept creation as expressed indirectly through natural laws and directly through a Divine Hand, that is, naturally and supernaturally, also interpret the following as the antedeluvian (*sic*) civilization:

"There were giants in the earth in those days; and after that, when the Sons of God came in unto the daughters of men and they bare children to them, the same became mighty men which were of old, men of renown."

Evidently the "Sons of God" were Seth, and even Cain with all his sin,—the sons from God's special creation into whom the "breath of life" had been breathed; and the "Daughters of Men" were plainly those human forms from God's evolved creation. There is no definite account in God's infallible word that Adam and Eve were parents of daughters bearing names as did their sons and, even if it were true that they enjoyed such parenthood, it is unthinkable that their sons took for their wives their own sisters. Neither is there any scriptural record that the wives of Cain and Seth were fashioned from the bodies of these sons of Adam just as their mother was begotten from their father's rib.

This, we think, will be enough, indeed a plenty. No "reconciler," whether biologist, physicist, or parson, should be without a copy of Professor Utterback's handy pamphlet. We find it difficult to conceive how anything more completely suited to their purpose could be found. In current phraseology, it is swell.

EVOLUTION BY SYMBIOSIS.
*By H. Reinheimer.* *Grevett and Co., Ltd.*
15 shillings net *Surbiton, England*
$4\frac{1}{2} \times 6\frac{7}{8}$; 141

We have had occasion in these columns to give considerable attention to the productions of paradoxers, and have found the opportunity to point out the entertainment and instruction they frequently contain. The *opus* under consideration here, which is of the same genus but a different species from those previously noticed, cannot, we are sorry to say, be similarly recommended. It labors the thesis that the unmoral struggle for existence which biologists allege lies at the basis of evolution is perversely conceived, and that symbiotism and coöperation are really its guiding rule. The evidence given for this generality is frail, and, what is much worse, is advanced with a terrible earnestness that deprives it of the all saving grace of humor.

OLD MOTHER EARTH.
*By Kirtley F. Mather.*
*Harvard University Press*
$2.50 5½ x 8; xiv + 177 *Cambridge*

This book has developed out of a series of radio talks on geology given by the author at Boston in 1927–1928. Naturally it is for the general reader. Not only geology but the origin of life and the evolution of mankind are presented in an engaging manner. The text is enriched by 61 illustrations.

## GENETICS

DAIRY CATTLE BREEDS. *U. S. Department of Agriculture Farmers' Bulletin No. 1443.*
*By Amer B. Nystrom.*
*Government Printing Office*
5 cents *Washington, D. C.*
6 x 9½; 29 (paper)

In this bulletin are discussed the number and distribution of the different dairy breeds in the United States, their origin and development and the chief characteristics of each. Suggestions are included concerning the factors to consider in selecting a breed. With the description of each breed a scale of points for a cow in use by the breed association is given. There are twenty-one illustrations of famous bulls and cows and a number of tables exhibiting the butter-fat and milk production of pedigreed animals.

THE LIVESTOCK REVIEW FOR 1927. *United States Department of Agriculture Miscellaneous Publication No. 28.*
*By H. M. Conway.*
*Government Printing Office*
10 cents *Washington, D. C.*
5¾ x 9⅛; 44 (paper)

"This review is designed (1) to give a perspective of basic conditions in the livestock industry, (2) to point out and emphasize the short-time variations and the general trend of market supply and demand and resulting prices during 1927, (3) to present a general interpretation of the livestock situation, and (4) to indicate the basis for some of the statements appearing in The Agricultural Outlook for 1928."

## GENERAL BIOLOGY

BIOLOGICAL CHEMISTRY AND PHYSICS OF SEA WATER.
*By H. W. Harvey. The Macmillan Co.*
$4.25 5½ x 8½; x + 194 *New York*

This useful treatise, written to fill the gap in oceanographic literature between the publication of *The Depths of the Ocean* in 1912 and the beginning of current bibliographies in 1926 in the *Journal du Conseil International pour l'Exploration de la Mer*, will be found interesting by the general biologist as well as the specialist in oceanography. It discusses the sea as the environment of plants and animals, maintaining throughout a primarily biological viewpoint, though the details of the discussion are of physical and chemical matters. The topics treated are: Chemistry of sea water; water movements (tides and currents); temperature of the sea; color and illumination of sea water; chemical and physical factors controlling the density of population. There are bibliographies for each of these topics.

NATURAL HISTORY OF CANTERBURY. *A Series of Articles on the Early History of the Province and on the History of*

*Scientific Investigation, up till 1926, as well as on some Results of this Investigation.* *Philosophical Institute of Canterbury*
17 s. 6 d. *Christchurch, New Zealand*
5¼ x 8; 299

Canterbury Province of New Zealand—a natural unit in that it is between high mountains on one hand and the sea on the other and has a special climate and geological history—has been the leading agricultural area in New Zealand ever since it was founded seventy-five years ago. In this volume The Philosophical Institute of Canterbury has issued a series of articles on the early history of the Province and on the history of scientific investigation up to 1926, as well as on some results of these investigations.

It was on a sheep farm in the sub-alpine region of Canterbury that Samuel Butler dwelt for four years, obtained the background of Erewhon, and carried on his controversy with the Bishop of Wellington. It was in this region also that Robert Brown, a shoe maker by trade in Glasgow until the age of 52, made his intensive studies of mosses and ferns, his equipment being an old-fashioned microscope and a home-made camera lucida. Sir Julius von Haast, the geologist, who lived here from 1860 to the time of his death in 1887, contributed many articles on the geology of Canterbury and was founder of the museum. Frederick Wollaston Hutton, in his early years a geologist, worked chiefly in New Zealand on zoology and the geographical relations of the New Zealand fauna.

It is around such pioneers as these that the book is written. The articles have been made as free of technicalities as possible in order that the lay reader would not find the book forbidding. Since each contributor is an authority in his field the book contains much information that is not otherwise accessible to the student of natural history.

There is a table of contents and 27 illustrations, but unfortunately no index, which decidedly reduces its usefulness to the student.

METHODIK DER WISSENSCHAFTLICHEN BIOLOGIE. *Erster Band: Allgemeine Morphologie. Zweiter Band: Allgemeine Physiologie.*
*Edited by T. Péterfi.* *Julius Springer*
188 marks (paper) for two volumes *Berlin*
198 marks (cloth) for two volumes
6¾ × 10¼; Vol. I, xiv + 1425
Vol. II, x + 1219

This large treatise on biological technique is stated by the editor to be needed in addition to the great Abderhalden *Handbuch* on the same subject because the latter is too large and too detailed. Doubtless the present work will serve a useful purpose, particularly for laboratories which cannot afford to purchase the larger work. Even for these, however, it will be no easy task to buy this treatise. Its price in paper is approximately $47. Our guess is that few American laboratories except the larger ones will feel that they can afford it.

The material is divided between the two volumes on the basis of morphology and physiology. The separate chapters are contributed by some forty odd specialists. The choice of subjects is good and the editing has been well done. Wherever we have had occasion to consult it in connection with the routine work of the laboratory we have found the indexing so good as to make it possible quickly to find what is wanted, and the information has been presented in sufficient detail to be practical. We congratulate the editor, Dr. Péterfi, on his enterprise in putting through so considerable a task so well, but we wonder at the economics of the

business. Perhaps the law of diminishing returns no longer operates in Germany.

THE SOCIAL INSECTS. *Their Origin and Evolution.*
*By William Morton Wheeler.*
*Kegan Paul, Trench, Trubner and Co., Ltd.*
21 shillings net *London*
5½ x 8½; xviii + 378

The French edition of this notable book was reviewed *in extenso* in THE QUARTERLY REVIEW OF BIOLOGY by Professor Philip P. Calvert (Vol. II, pp. 119–124). The author states that:

> In preparing this English edition I have retained the original lecture form, but several passages, which had to be omitted in order to bring the volume within the requirements of the French publisher, have been restored to the text, a number of typographical and other errors have been corrected and a small amount of new material has been added. I have also introduced several new illustrations and have omitted a few of those in the French edition. In its present form the work has been brought up to date so far as this was possible without unduly expanding the text and the bibliography.

It is a great service to biology to have this learned and entertaining volume available in English.

THE SEAS. *Our Knowledge of Life in the Sea and How it is Gained.*
*By F. S. Russell and C. M. Yonge.*
*Frederick Warne and Co., Ltd.*
12 s. 6 d. net *London*
4½ x 6⅛; xiii + 379

This attractive "handy volume" with its numerous illustrations (there are 384, of which 167 are in full color) will be particularly interesting to the lay reader whose hours of recreation are spent near or on the sea. The authors, both of whom have been connected with the Marine Biological Association at Plymouth, England, have a wide acquaintance with the fauna and flora of the ocean. Within the covers of this book they give the best popular account of oceanography, in its broadest sense, that we have seen. The illustrations are largely new and well chosen. If the book were to appear devoid of text it would still be well worth possessing because of them. There is an index.

JAHRESBERICHT ÜBER DIE WISSENSCHAFTLICHE BIOLOGIE. *Zugleich Bibliographisches Jahresregister der Berichte über die Wissenschaftliche Biologie. Band I. Edited by Tibor Péterfi.* *Julius Springer*
69 marks *Berlin*
7 x 10¼; xii + 627 (paper)

The first volume of a new bibliographic enterprise, of interest to all biologists. It lists the biological titles from some 1328 journals of all parts of the world. All titles listed are of the year 1926. The typographical treatment is good; each title so far as possible apparently carries the useful item of the author's address; there is good cross-referencing. We confess to liking the classification better than that of *Biological Abstracts* in a number of particulars. Altogether we are inclined to predict that this new *Jahresbericht* will succeed if it maintains its initial standard.

THE IDEA OF MEMORY IN BIOLOGY. *Being the Tenth Earl Grey Memorial Lecture Delivered at King's Hall, Armstrong College, Newcastle-on-Tyne, March 2, 1928.*
*By E. W. MacBride.*
*Oxford University Press.*
35 cents 6 x 9; 27 (paper) *New York*

Professor MacBride, as every one knows, is an ardent Lamarckian. This lecture is about the inheritance of acquired characters. It chiefly discusses the experiments of Dürkhen and Heslop Harrison upon the coloration of insects; color and other adaptations of amphibia; and some of the recent work in experimental embryology, notably that of Spemann. The odd thing is that in this whole lecture devoted to the idea of memory in biology not one single mention is made of either Hering, Samuel Butler, or Semon! And what is perhaps still odder is that a careful perusal of the lecture fails to discover in it one single "idea" about memory in biology which has not already been discussed in one form or another by one or more of these three persons.

AN INTRODUCTION TO OCEANOGRAPHY. *With Special Reference to Geography and Geophysics.*
*By James Johnstone.*
*Hodder and Stoughton, Ltd.*
15 shillings net *London*
5½ x 8½; xi + 368 + 4 maps

This revised edition of Professor Johnstone's outline of oceanography should be of interest to a wide range of readers. There are chapters on the origin of the oceans, the depths of the ocean, the sea bottoms, the oceanic margins, the chemistry of sea water, the physical characters of sea water, the tides, the oceanic circulation, and secular changes in the ocean. The treatment is general, and the attempt has been to provide an introduction to all the important aspects of oceanography. There is an appendix giving a list of the principal authorities consulted, and a good index.

KRITISCHE THEORIE DER FORMBILDUNG. *Abhandlungen zur theoretischen Biologie. Heft 27.*
*By Ludwig Bertalanffy.*
*Gebrüder Borntraeger*
14 marks *Berlin*
6⅜ x 10; vi + 243 (paper)

A critical discussion of the present state of knowledge of morphogenesis, prefaced by a hundred pages regarding theoretical biology in general. The general conclusion reached is that there is no evidence in what we know of embryonic development for the existence of any specific form producing or controlling factor. Form, on the contrary, is a *primary* characteristic of living organisms. This is a well written, interesting and stimulating discussion of the fundamental problems of biology.

MEASUREMENT OF SALINITY OF SEA WATER. *Department of Commerce, U. S. Coast and Geodetic Survey Special Publication No. 147.*
*By Jerry H. Service.*
*Government Printing Office*
10 cents *Washington, D. C.*
5⅞ x 9¼; iii + 20 (paper)

In this publication is presented the preliminary calibration of the dipping refractometer as well as a study of other methods available for use on board ship for measuring the proportion of total dissolved solids in sea water. In the text are 8 illustrations, 3 charts and 5 tables.

FUNDAMENTALS OF BIOLOGY.
*By Arthur W. Haupt. McGraw Hill Book Co.*
$3.00 5⅝ x 9; xii + 358 *New York*

This elementary text for the use of beginning classes in general biology soundly follows conservative lines. Roughly half the book deals with morphological matters, and the rest with such general topics as genetics, ecology, evolution, etc. It is sufficiently well illustrated and indexed.

GENERAL BIOLOGY.
*By Leonas L. Burlingame, Harold Heath, Ernest G. Martin and George J. Peirce.*
*Henry Holt and Co.*
$3.50 5½ x 8½; xxx + 597 *New York*

A text book for use in an introductory course for college students. It is planned on the idea of stressing principles rather than factual details, and demands very little equipment in the collateral sciences for its comprehension.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN Lieferung 271. *Einrichtung von Zimmer- und Freiland-Aquarien und -Terrarien einschliesslich der Technik der Haltung und Zucht von Fischen, Reptilien und Amphibien.*
*By Wilhelm Klingelhöffer.*
*Urban und Schwarzenberg*
24 marks 7 x 10; 456 (paper) *Berlin*

This fascicle of the Abderhalden handbook contains by all odds the most thorough and comprehensive discussion of small aquarium and terrarium technique that we have seen.

THEORETISCHE BIOLOGIE.
*By J. von Uexküll.* *Julius Springer*
15 RM (Paper) *Berlin*
16.80 RM (Cloth)
6⅜ x 9½; x + 253

The first edition of this book, in English translation, has been noted in this REVIEW (Vol. II, No. 2). This issue, *gänzlich neu bearbeitet*, does not appear to contain anything essentially new.

PLANKTONKUNDE. *Eine Einführung in die Ökologie der im Wasser Schwebenden Kleinwelt.*
*By Wilhelm Heesen.* *Otto Salle*
2.80 marks 5½ x 7½; xi + 90 *Berlin*

A very satisfactory little text designed as introductory to the study of plankton. For further investigation a list of more exhaustive references is provided.

BLOOD. *A Study in General Physiology.*
*By Lawrence J. Henderson.*
*Yale University Press*
$5.00 6 x 9; xix + 397 *New Haven*

A long review of this notable book will appear in the next number of THE QUARTERLY REVIEW OF BIOLOGY.

## HUMAN BIOLOGY

THE TWILIGHT OF THE AMERICAN MIND.
*By Walter B. Pitkin.* *Simon and Schuster*
$3.00 5⅜ x 7⅞; xviii + 362 *New York*

The orthodox eugenic creed contains two main articles: first, that the inferior sorts of men should be discouraged, perhaps forcibly restrained, from breeding, and second, that the superior sorts of men should be encouraged to breed more rapidly. There is here a threat and a promise: unless we subscribe to Article 1, the world will be entirely populated by morons in 1987, or some such date;

and if we subscribe to Article 2, the average man of 1962 will possess Galton's I.Q., Voltaire's literary style, Schubert's musical talent, and so on.

The present volume is not concerned with the first of these canons, nor does it deal with the possibility of carrying the second into execution. The author limits himself to the question of whether it is really desirable to produce a great many more highly intelligent people than now exist; and he deals with this question purely on the basis of finding jobs for these superior people. He makes, in short, a survey of the various occupations of the United States, and estimates the number of jobs which require high intelligence if they are to be done properly. His conclusion is that we already have a surplus of intelligence, and that this surplus is growing, not shrinking; and we believe that he has pretty well backed up his conclusion with sound evidence as well as clever and amusing dialectic.

We suspect that this book will be very lightly esteemed by the eugenists, but we commend it highly to their earnest consideration. For it poses a number of questions which no eugenist who wants to be considered as more than a mere uplifter can afford entirely to neglect. Pitkin's view of the direction of evolution of society seems to us in general sound: namely, that society is requiring less and less intelligence to keep it going. If this is so, what is the evolutionary use of trying to increase the number of highly intelligent people?

Finally, we may remark that Pitkin's technique has a much wider application than merely to a particular phase of eugenic propaganda. It may, we think, be applied to the uplift in any of its forms. In short, no program of the uplift is worth the paper it is written on unless it is based on a realistic consideration of all the relevant facts, and unless it includes a realistic study of all the consequences which may follow from its adoption. So far as we know, no uplifter has ever presented that kind of program; and we do not expect that any uplifter ever will.

THE PROMOTION OF THE WELFARE AND HYGIENE OF MATERNITY AND INFANCY. *The Administration of the Act of Congress of November 23, 1924. Fiscal Year Ended June 30, 1927. U. S. Department of Labor Children's Bureau Publication No. 186.*

*Government Printing Office*
25 cents *Washington, D. C.*
$5\frac{7}{8}$ x $9\frac{1}{4}$; vi + 150 (paper)

This volume reached the editorial desk along with the editorial income tax blank; not unnaturally. Therefore, we have made an attempt to discover just what has actually been accomplished by the operation of the Sheppard-Towner Act. On pages 2 and 3 we find a table which shows a total of $4,697,234.86 of Federal funds accepted by the states. This, however, is not the full amount spent, since under the Act most of this must be matched dollar for dollar by the states. The total of Federal and State expenditures we work out to be something over eight million dollars.

Eight million dollars seems to us like a lot of money; what have we got for it, outside of creating some pleasant places for jobholders? Examining the succeeding tables, we find that during the year ended June 30, 1927 there were held a total of 33,783 conferences at which 29,041 mothers and expectant mothers and 227,733 children were registered, inspected, advised, and instructed. In the same period there were also conducted 1196 classes in which 26,356 mothers

were enrolled, etc.; that a total of 18,207 talks and lectures, including 110 radio broadcasts, were given to 408 physicians, 794 nurses, 13,442 laymen, and the uncounted millions of the radio audience; that 46,217 sets of prenatal letters were sent out; and that the total of "pieces of literature distributed" was 4,403,218.

We see that the jobholders have not been idle; and it was with something of a thrill that we turned to the section "Some Results of Five Years of Work." Here, said we, we shall learn what all this has accomplished. So we looked eagerly through some remarks about "Expansion of Activities" and "Increase in State Appropriations for Child-Hygiene Work," until we come to the heading "Reduction in Infant Mortality." Here we are given a table which really shows what we want to know. It gives the average infant mortality rates by states for the years 1917–1921 (exclusive of 1918) and 1922–1926—before and after the act took effect. Further, we are able to compare the course of affairs in the coöperating states with those not coöperating. No averages are given in the table, but it is easy to compute them; which we did, with the result here given:

| | *Infant mortality* | | |
|---|---|---|---|
| | 1917–21 (1918 omitted) | 1922–26 | *Percent decrease* |
| 16 coöperating states | 80.07 | 71.56 | 10.6 |
| 5 non-coöperating states | 84.96 | 73.18 | 13.9 |

This result, we may say, distressed us greatly; and accordingly we tried to see what could be done about it. Our figures are simply flat averages of the rates given in the table; but we have also tried weighting them by the population of the states, and we have tried omitting certain states which either did not come into the Birth Registration Area until 1919 or which did not begin coöperating until 1923. However, no treatment of the figures has altered the conclusion which we should draw from the table above—namely, that eight million dollars of the tax payer's money has been spent with precisely no effect at all on the course of infant mortality.

AN INTRODUCTION TO THE STUDY OF SOCIETY. *An Outline of Primary Factors and Fundamental Institutions.* *By Frank H. Hankins. The Macmillan Co.* $4.00 5½ x 8½; xiii + 760 *New York*

A text book for use in a general survey course in sociology. It covers, as one might expect, a great deal of ground, much of it properly belonging to other sciences; and it is not to be expected that specialists will agree in all cases with the author's use of material from their fields. He has plainly endeavored to maintain a properly dispassionate and scientific attitude toward human problems, but occasionally slips into pious hopes for uplifting the race. There are, after all, few writers with the detachment of Pareto—who, incidentally, is not mentioned in this book.

Some of the "questions for discussion and further study" appended to the various chapters are, we should say, tall orders. For example, the following from Chapter VII. p. 318;

4. What is the selective value of war?

5. Suggest a practical plan for greatly reducing the proportion of morons in our population.

9. How is selection related to vestigial organs? How would you explain the blindness of fishes living in caves?

12. Is modern charity and philanthropy justifiable?

15. In what ways and to what extent does a race acquire immunity to germs and diseases to which it is constantly subjected?

16. What are the causes of the decline in the birth rate in the past fifty years?

19. Why should births following a war show an unusual proportion of males?

20. If it could be proven that alcohol acts selectively so as ultimately to produce a race immune to its effects, would this warrant its unrestricted use in modern society?

There are references following each chapter; those for chapter VII are the following:

SUGGESTED READINGS

Davis-Barnes: *Readings in Sociology*, pp. 398–480.
Bushee: *Principles of Sociology*, Chap. 24, pp. 386–413.
Carr-Saunders: *The Population Problem*, Chaps. 5, 7, and 11, pp. 88–105, 135–161, and 270–307.
East: *Mankind at the Crossroads*, Chaps. 5, 6, 8, and 9, pp. 110–198 and 231–283.
Holmes: *Trend of the Race*, Chap. 8, pp. 181–204.
———: *Studies in Evolution and Eugenics*, Chaps. 7–9 and 11, pp. 134–169 and 179–188.
Newman: *Evolution, Genetics and Eugenics*, Chaps. 17 and 19, pp. 237–249 and 276–293.
Wiggam: *The Fruit of the Family Tree*, Chap. 18, pp. 304–316.
Wolfe: *Readings in Social Problems*, Chaps. 1 and 2, pp. 17–117.
Wright: *Population*, Chaps. 2 and 6, pp. 20–39 and 99–118.

ADDITIONAL SELECTED REFERENCES

Carr-Saunders: *Population*, entire.
Castle: *Genetics and Eugenics*, Part IV, pp. 331–375.
Darwin: *The Need for Eugenic Reform*, Chaps. 17, 18, and 22, pp. 295–327 and 391–415.
East: *Heredity and Human Affairs*, Chap. 13, pp. 247–265.
Lennes: *Whither Democracy?*, Chaps, 7–9, pp. 252–332.
Popenoe and Johnson: *Applied Eugenics*, Chaps. 6, 8, and 9, pp. 116–146 and 167–183.
Siemens: *Race Hygiene and Heredity*, Chap. 10, pp. 130–154.
Sorokin: *Social Mobility*, Chaps. 10–13, pp. 215–333.

Without disrespect to these authors, we should like to know how many of these questions students will find answered. In fact we should like to have the answers to one or two of them ourselves.

COMING OF AGE IN SAMOA. *A Psychological Study of Primitive Youth for Western Civilization.* *By Margaret Mead.* *William Morrow and Co.* $3.00 5¼ x 8; xv + 297 *New York*

This book has been a "best seller," in spite of the fact that it was written as a serious contribution to anthropology, done under the auspices of the National Research Council, and introduced by Professor Franz Boas. Its large popular sale has been due, we incline to think, to two causes: it is well written, and there is a lot in it about sex.

Looked at solely as a piece of research the first point to be noted is that Miss Mead spent altogether nine months in Samoa, six months of them upon the little island of Taū in the Manu'a Archipelago. During this time she had to learn the language, and collect the data for the study, which included the most extensive probing into the intimate private lives of all the women and girls, and some of the men, in three villages. Doubtless the Samoan language is an easy one to learn, and evidently Miss Mead must be an extraordinarily facile linguist, but making all allowance in both these directions one can but marvel at the range of material covered in the research. When one recalls the testimony of such men as Westermarck and Stefansson for example, that only after years of living with natives did they *really* get "inside" their lives and thoughts it raises a query as to whether Miss Mead penetrated as deeply into the secrets of the Samoan ladies as she thought she did.

The main point brought out by the study is that girls in Taū have fewer inhibitions about sex, and various other crudely biological matters, than do girls in the United States. Broadly speaking, this is no doubt true. But what, precisely, of it? Social customs and attitudes are, taken by and large, adaptive responses to the whole biological and physical environment. When they cease to be adaptive

they are apt to change. The sex behavior of the girls and boys of Taū would be less well adapted to a New York City present day environment than is that of the youth of our great metropolis. In spite of the author's rather prolix exposition of her moral judgments and wishes in the matter, we make bold to doubt if the behavior of either group is likely to be very helpful in guiding the behavior of the other.

With the reservations which have been suggested as to the degree of seriousness with which the book is to be taken as a piece of scientific research, we can recommend it heartily as entertaining reading.

ARCHÆOLOGICAL INVESTIGATIONS IN KAMCHATKA. *Carnegie Institution of Washington Publication No. 388.*
*By Waldemar Jochelson.*
*Carnegie Institution of Washington*
$2.75 (paper) *Washington, D. C.*
$3.75 (cloth)
$9\frac{1}{8}$ x $11\frac{1}{2}$; viii + 88 + 19 plates

This publication, together with a previous one on Archaeological Investigations in the Aleutian Islands, also issued by the Carnegie Institution of Washington, represents part of the results of an investigation carried on by the author in 1910–11 under the auspices of the Imperial Russian Geographical Society. The present volume deals very largely with the implements, weapons and pottery of the early Kamchadal inhabitants, but in addition there is a discussion of the history of Kamchatka and the Stone Age in Siberia and adjacent countries. The author hesitates to link his findings up with any particular age or era. He concludes that during the early Kamchadal history the country was densely populated, the inhabitants living during the winter months in pit-dwellings (abodes in the earth) and in summer in huts on piles several meters high.

There are numerous illustrations of the objects excavated, these coming very largely from pits in the vicinity of Kuril Lake.

In addition to the 19 plates and a map of Northern Asia exhibiting the distributions of palaeolithic, neolithic, bronze and iron stations of Siberia there is a lengthy bibliography and index. The volume is issued in superb form.

HUMAN MIGRATION AND THE FUTURE. *A Study of the Causes, Effects and Control of Emigration.*
*By J. W. Gregory.*
*Seeley, Service and Co., Ltd.*
12 s. 6 d. $5\frac{1}{2}$ x $8\frac{1}{2}$; 218 *London*

The central thesis of this book is that human migration is beneficial, both to the countries that lose and to those that receive the wanderers. The distinguished author, who is Professor of Geology in the University of Glasgow, argues that there is still plenty of room in temperate regions of the globe for all those who want to emigrate from European countries. In his view migration offers something approaching a solution of the world population problem. He discusses birth control only as an alternative to emigration, and appears to regard it with disfavor. He hopes that "the European race may not be forced to methods of birth control that would increase its numerical inferiority to the coloured races."

The book is well documented and indexed, and will interest all students of human biology.

THE INTERPRETER GEDDES. *The Man and His Gospel.*
*By Amelia Defries.* *Boni and Liveright*
$3.00 5½ x 8½; xiii + 334 *New York*

Patrick Geddes is without doubt one of the most remarkable men of our times. Many years ago when the reviewer was a graduate student Geddes spent a morning with him watching and discussing the experiments in progress, and the memory of his eager, vivid personality has always remained fresh. His versatility has been extraordinary. As biologist, sociologist, botanist, philosopher, town planner, and all-round human being he has everywhere left his mark.

To our taste, at least, this book does not do Geddes justice. Somehow he would seem to deserve something better biographically than the turgid adulation of a very feminine hero-worshipper. However, in the absence of anything better, all biologists will be interested in reading this. Some idea of the wide range of Geddes' interests may be gained from the chapter headings, which are as follows: The Masque of Learning; The Cities and Town Planning; The Outlook Tower; The Returning Gods—Olympus; The Notation of Life—Parnassus; Geddes in his Garden; A Botanist Looks at the World; Art and Sex; Cities in Devolution; Education, Politics, Housing; Scotland and France; Jerusalem; Montpellier; Last Words; Five Friendly Critics.

There is a foreword by Rabindranath Tagore, a preface by Lewis Mumford, and an introduction by Israel Zangwill. A selected bibliography of Geddes' writings ends the book. There is no index.

THE FORMATION OF THE CHINESE PEOPLE. *An Anthropological Inquiry.*
*By Chi Li.* *Harvard University Press*
$5.00 7 x 10¼; 285 *Cambridge*

This book is an attempt to determine the origin of the modern Chinese through anthropological, archaeological, and historical investigations. The author begins with a study of the physical traits of the modern Chinese. He then investigates the building of city walls in different provinces, with the general thesis that the earlier the period of greatest building activity, the earlier was the occupation of the province by the Chinese. He then investigates the origin and migration of the Chinese as indicated by the locality of occurrence of ten typical surnames. He then considers the barbarians with whom the Chinese have been in contact, and their relations with the Chinese. In a final chapter he considers the various elements whose integration has resulted in the modern Chinese.

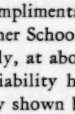
It is not always easy to follow the author's argument, partly because his expression is not as clear as might be wished. We own to a certain scepticism as to the value of some of his results, especially those based on the history of surnames; but our ignorance of things Chinese prevents our expressing a critical judgment on most of the book. It is fair to say, however, that the author has been quite ingenious in developing statistical methods for handling his historical material.

The book seriously lacks an index.

SECONDARY SCHOOL EXAMINATION STATISTICS. *Prefaced by a Simple Introduction to Statistical Methods.*
*By J. M. Crofts and D. Caradog Jones.*
*Longmans, Green and Co., Ltd.*
$1.00 4⅞ x 7½; 88 *New York*

A brief account of the machinery of School Certificate Examinations in England, with some statistical discussion of the results. There is an excellent introductory chapter on the statistical analysis of examination results, written especially for the non-statistical reader; and chapters on the School Certificate and Higher School Certificate examinations. The analysis indicates that at age 16

> the average girl is the equal, if not the superior, of the average boy, but that taken all round girls show less variation than boys. They may be regarded in the mass as more steady or more humdrum, according as we wish to be complimentary or otherwise. At the stage of the Higher School Certificate two years later—that is, roughly, at about 18½ years of age—the difference in variability has increased, and the superiority previously shown by the girls in certain subjects has vanished altogether, while in others it shows signs of decreasing, indicating that girls cannot compete on equal terms with boys in academic tests of the standard in question. But it is important to note that this is only true of boys and girls in general: there appear from time to time exceptional girls who can on equal terms, compete with and beat the best boys of their year at least in some subjects.



THE SOCIOLOGY OF LIFE INSURANCE.
*By Edward A. Woods. D. Appleton and Co.*
$2.50 5¼ x 8; xix + 331 *New York*

The title of this book is misleading. It actually consists of high-toned language for the insurance salesman. A sample:

> The idle rich and the thriftless masses are the menace of any nation. They were in Babylon, Assyria, Persia, Greece, and Rome in antiquity, and in France at the time of the Revolution. They are even so in America to-day.
>
> A great institution that is encouraging more than a majority of the entire population to practice systematic thrift over a long period of years or a lifetime and so to form habits that foster other ways of saving is of great social, economic, and even spiritual value to the nation.

THE PASSING OF THE FRISIANS. *Anthropography of Terpia.*
*By D. J. H. Nyèssen. Martinus Nijhoff*
7.50 guilders 6¼ x 9½; 296 *The Hague*

This book is a study of the early inhabitants of the terps or mounds of the northern coastal region of Holland. A great part of the book is taken up with craniometric investigations, from which the author concludes that the inhabitants of the Friesland terps were racially differentiated from those of the Groningen terps. Whether he is justified in this conclusion we cannot say; because the statistical treatment of the material is grossly defective. His procedure throughout is to compare two distributions, with their means and ranges (and we have not always been able to check his computation of the mean), and to assert that they are different or similar on the basis of inspection. There is nowhere a test of goodness of fit: there is not even a mention of a probable error. And yet we find him saying: "The value of many a protracted inquiry performed in Holland, has been less than might have been expected, on account of an *insufficient knowledge of method, and also of statistics.*" (The author's italics).

We ought, however, to say that he has given the actual frequency distributions, so that anyone who wishes to apply proper statistical methods to the data may do so.

DENTITION AS A MEASURE OF MATURITY. *Harvard Monographs in Education No. 9.*
*By Psyche Cattell. Harvard University Press*
$1.00 *Cambridge*
6¾ x 10; viii + 91 (paper)

The purpose of this study is to establish standards of physical development on the

basis of the state of eruption of the teeth. The subject is briefly reviewed and the standards previously developed criticized. The authoress proposes as a result of her own investigations, standards that depend on the total number of teeth present rather than a method of weighting by the particular type of teeth or the degree of eruption. There is a consideration of sex and race differences, and finally it is advocated that the dental standards be combined with others, such as those based on anatomical measurements and carpal development, into an index of general physical maturity. We are not impressed with the wisdom of this last suggestion. The correlations between the ages estimated by the different standards are low, indicating, so far as these standards refer at all to physical development, that development in one system does not proceed *pari passu* with that of another. To combine the different measures into a simple index would therefore tend to obscure rather than to increase their utility.

PREHISTORIC MAN.
*By Keith Henderson. E. P. Dutton and Co.*
$3.00 5½ x 8; xv + 276 *New York*

A popular account of early man, intended for the general reader. It forms one number of the "Simple Guide" series, published in this country by Dutton. It is abundantly, and rather well, illustrated with line drawings by the author. It contains nothing new, and a good deal of the purely speculative generalization in which popular writers on prehistoric man are so inclined to indulge. And how fond such writers are of using nice, juicy words, without stopping to think precisely what they mean. For example Mr. Henderson says on p. 47: "Another important Mousterian is a middle-aged male from La Chapelle aux Saints. Here again we get that impression of heavy strength in a body still redolent of the beast." Now to be "redolent" is to be "full of or diffusing a pervasive odor; especially, smelling sweet or agreeable." We doubt that the Chapelle skull exhales any odor of the beast, sweet or otherwise.

THE EMPLOYMENT OF WOMEN AT NIGHT. *Bulletin of the Women's Bureau, No. 64.*
*By Mary D. Hopkins.*
*Government Printing Office*
Free *Washington, D. C.*
5¾ x 9; 86 (paper)

This report deals not only with the conditions of night employment in the United States but also with the protective legislation for women in foreign countries. Included in the report is the text of the Bern and Washington conventions. Considerable space is devoted to a discussion of the harmful effect of night work upon the physical condition of laborers, it being generally agreed that it is "disproportionately more harmful to a woman's physique than to a man's." Reading the testimony of various experts who have studied the employment of night labor from a purely economic point of view one is inclined to the view that at least some of the ills of industry would be mitigated if night work were abolished for both sexes.

PRESCRIBING OCCUPATIONAL THERAPY.
*By William R. Dunton, Jr.*
*Charles C. Thomas, Inc.*
$2.10 (cloth) *Springfield, Ill.*
$1.35 (paper)
4⅞ x 7⅛; 142

The definition of occupational therapy in the meaning of this little book is "any activity, mental or physical, definitely prescribed and guided for the distinct purpose of contributing to and hastening recovery from disease or injury." The author's experience has apparently been mostly in the field of psychiatry, but he has given much thoughtful attention to the subject in general. There is a short, not very searching discussion of principles, followed by separate chapters on specific applications to mental disorders, general medical, surgical, orthopedic, cardiacs, tuberculous, children, and bed occupations. There is an intelligent recognition that this form of therapy is only ancillary to general medical treatment, and from this view the book ought to be of help to the practicing physician.

THE PEOPLE OF THE TWILIGHT.
*By Diamond Jenness. The Macmillan Co.*
$3.00 5½ x 8½; 247 *New York*

The author spent two years among the Esquimaux of the Coronation Gulf Region and here recounts his experiences among them. He developed a great attachment for the people and tells of their manners and difficulties with deep sympathy and appreciation. In conclusion he laments the threatened extermination of this picturesque and happy folk by the action of invading traders. For the sake of the furs that may be secured, the natives are supplied with high power guns; by means of these the scant source of meat is soon exhausted, and the people starved to extinction.

The book is provided with an introduction by Fridtjof Nansen, and contains a number of illustrations as well as a map of the region traversed.

HUNGER FIGHTERS.
*By Paul de Kruif. Harcourt, Brace and Co.*
$3.50 5¾ x 8½; 377 *New York*

Last night the reviewer dined with a number of medical men, who were all of the decided opinion that *Hunger Fighters* was a much better book than *Microbe Hunters*. It seems to us not quite so good as that masterpiece. The reason is that, with a few exceptions—notably Mark Carleton—the men discussed in *Hunger Fighters* seem intrinsically less interesting and less significant men than those in *Microbe Hunters*. But after all, who are we to pass such a judgment? It is enough to say that Paul de Kruif has written another book about another group of biologists which every subscriber to this REVIEW will want to read. There is the same gusto, the same insight, and the same pungent and often subtle commentary on the history of science that made *Microbe Hunters* a great book.

HIDATSA EAGLE TRAPPING. *Anthropological Papers of The American Museum of Natural History. Vol. XXX, Part IV. By Gilbert L. Wilson.*

*The American Museum of Natural History*
$1.50 6½ x 9¾; 146 (paper) *New York*

An interesting account of the methods of trapping eagles used by the Hidatsa Indians, in the form of narratives by Wolf-chief, a Hidatsa born about 1849, and recorded in 1915. Eagle trapping was a ceremonial affair, with a complicated ritual; but apparently it was not unknown for somewhat irreverent young men to go out on their own and trap eagles with a minimum of attention to the formal observances officially prescribed. The first of Wolf-chief's narratives tells of such an expedition; the second tells of an eagle trapping expedition on which all

the rules were followed. Apparently there was no penalty attached to departures from tradition, nor even any serious objection on the part of the more orthodox members of the tribe.

MAN A MACHINE. *In Answer to a Romantical and Unscientific Treatise Written by Sig. Eugenio Rignano and Entitled "Man Not a Machine."*
*By Joseph Needham.*
*W. W. Norton and Co., Inc.*
$1.00 4⅛ x 6½; 103 *New York*

A well written little book, which, however, is not quite what the title would lead one to suppose. Most of the book is occupied in a refutation of Rignano's teleological argument for vitalism; but, having demolished Rignano, the author goes on to explain that he does not really mean that man is a machine, but only that unless he is a machine he cannot be treated scientifically, and that therefore science is compelled to assume that he is. But he at once concedes that this is fundamentally a methodological fiction, and admits the right of philosophers and theologians to consider man as anything else they like. The concession seems fair to us, but we understand that it rather galls Mr. Mencken.

A CENSUS OF EPILEPTICS KNOWN TO THE PUBLIC AUTHORITIES IN THE COUNTY OF SURREY.
*Permanent Committee on Epileptics*
*London*
8¼ x 13¾; 19 (mimeographed)

Figures as to the incidence of epilepsy in the general population are practically non-existent. The present paper gives the results of a census of epileptics known to the public authorities in the population of Surrey (including the County Borough of Croydon). The material includes reports on 726 epileptics, and has been tabulated with respect to age, sex, mental conditions, and physical defects. As a result of this investigation, it is estimated that there are something like 25,000 epileptics chargeable to the public authorities in England and Wales.

AN ANALYSIS OF MAGIC AND WITCHCRAFT. *A Retrospective Introduction to the Study of Modern Metapsychics. By C. W. Oliver.* *Rider and Co.*
15 s. net 6 x 9; xi + 244 *London*

An outline of the various magical beliefs and practices which have existed in historic times, mainly in Western Europe. The book is, according to the author, intended as an introduction to the study of metapsychics or, in more usual terminology, spiritualism; but we should be less than fair if we implied that belief in spooks is prominent in the book. However, we doubt that the book will be found of great value; the same thing has been done before and done better.

RASSENKUNDE DES SCHWEDISCHEN VOLKES.
*Edited by H. Lundborg.* *Gustav Fischer*
16 marks (paper) *Jena*
19 marks (cloth)
8 x 11; viii + 160 + 50 plates

The English edition of this important contribution to human biology has already been noticed in these pages. While this German edition is somewhat condensed it is not harmfully so. Furthermore it contains some material not in the original English edition. It is a work of first rate importance and enduring value.

CANNIBAL JACK: *A True Autobiography of a White Man in the South Seas.*
*By William Diapea (Printed from the manuscript in the possession of the Rev. James Hadfield, with a foreword by H. de Vere Stacpoole).* *Faber and Gwyer, Ltd.*
7 s. 6 d. net *London*
$5\frac{1}{8}$ x 8; xxii + 242

We are not going to commit ourselves as to the veracity of this narrative. It purports to be a fragment of the autobiography of a South Sea trader, covering a period in the eighteen-forties. There is a glowing preface by H. de Vere Stacpoole, who rates the book with *Omoo* and *Typee*, which is a matter of opinion. Frankly, we did not get much of a kick out of the book.

OBSERVATIONS ON HUMAN HEREDITY.
*By J. S. Manson.* *H. K. Lewis and Co., Ltd.*
6 s. net *London*
$5\frac{3}{8}$ x $8\frac{1}{2}$; ix + 84

The greater part of this book is taken up with pedigrees of various abnormalities. The most valuable, because most complete, are those on hereditary lamellar cataract and on hereditary syndactylism and polydactylism.

THE BANTU TRIBES OF SOUTH AFRICA. *Reproductions of Photographic Studies. Vol. I, Section I, Plates I–XX. The Bavenda.*
*By A. M. Duggan-Cronin (with an introductory article on the Bavenda and descriptive notes on the plates by G. P. Lestrade).*
*Deighton, Bell and Co., Ltd.*
*Cambridge*
15 shillings (postage 6 pence)
$8\frac{1}{8}$ x $11\frac{1}{2}$; 23 + 20 plates (paper)

A short description of the Bavenda, and twenty excellent reproductions of photographs. When completed this will be an extremely valuable anthropological reference work.

PREHISTORIC MAN. *Reading with a Purpose (No. 43).*
*By George G. MacCurdy.*
*American Library Association*
Cloth, single copy, 50 cents *Chicago*
10 or more copies, 45 cents each
Paper, single copy, 35 cents
4 copies, $1.00
10 copies, $2.25
25 copies, $4.50
50 copies, $6.50
100 or more copies, 11 cents each
$4\frac{3}{4}$ x $6\frac{7}{8}$; 45

A very brief sketch of prehistory, with a useful short selection of books for the general reader.

## ZOOLOGY

THE BRITISH SEA ANEMONES.
*By T. A. Stephenson. Printed for the Ray Society. Sold by Dulau and Co.*
£1:17:6 *London*
$5\frac{1}{2}$ x $8\frac{5}{8}$; xiv + 148 + 14 plates

"The material presented here has been derived partly from a personal investigation of Actinian anatomy extending over a number of years, and dealing with species from many parts of the world as well as with those of the British area. This has been supplemented by an extensive study of living material, including not only attention to the external form of the living animal, but also an investigation of the methods of reproduction prevalent within the group, together with general

observation of natural history." The descriptions have been written direct from living animals, with the aid of a binocular dissecting microscope, and the notes on the range of variation given under each species are based largely upon personal experience. The book deals with the sub-order Actiniaria only, and does not include the Ceriantharia and Zoanthinaria.

It might be misunderstood from the title that the book is mainly taxonomic; more than half is devoted to a general account under the headings of structure, coloration, development, bionomics, and classification. Following are a list of British Actinaria, a list of the literature and an index of technical terms. The book is generously illustrated and contains a number of beautiful colored plates. We are delighted with Neptune's daughter as figured in the end pieces.

FIELD BOOK OF NORTH AMERICAN MAMMALS. *Descriptions of every mammal known north of the Rio Grande, together with brief accounts of habits, geographical ranges, etc.*

*By H. E. Anthony.* *G. P. Putnam's Sons*
$3.50 $3\frac{7}{8}$ x $6\frac{3}{4}$; xxv + 625 *New York*

In this book are collected, in condensed form, all of the important faunistic data concerning North American mammals, both land and marine. For each large group of mammals there is a full and detailed description with brief synopses of the other related forms. The 32 colored plates and 200 other illustrations are well chosen as an aid for studying the different types.

With this manual at hand the layman will have little difficulty in identifying most of the species and subspecies of mammals which he meets anywhere in North America north of the Rio Grande. The descriptions, common names, ranges, etc. are in terms which he can easily comprehend. Even the specialist on mammals will find this a useful book to have at hand. There are indices of both Latin and common names, a lengthy bibliography and distribution maps.

THE ECOLOGY OF AN HAWAIIAN CORAL REEF.

*Bernice P. Bishop Museum Bulletin 45.* *By Charles H. Edmondson.* *The Museum*
$1.00 $6\frac{7}{8}$ x 10; 64 (paper) *Honolulu*

The report of an intensive ecological study of a section of Waikiki reef. In addition to the field work experimental work was carried on on twenty-three forms of corals inhabiting this section. The principal point of attack was the problem of the responses of the coral animals to various environmental factors, notably temperature, salinity, silt, sunlight, etc. The range of variation in conditions which the animals are able to survive is not so wide as might have been expected *a priori*, save in the case of salinity of the water, where there is an extensive range of adaptability. Altogether this is a thorough and interesting piece of research.

BIBLIOGRAPHY OF SPONGES, 1551–1913.

*By G. C. J. Vosmaer. Edited by G. P. Bidder and C. S. Vosmaer-Röell.*
*The Macmillan Co.*
$5.25 $5\frac{3}{8}$ x $8\frac{5}{8}$; xii + 234 *New York*

This extensive bibliography which was begun in 1880, was unfinished at the time of the author's death in 1916. The manuscript has been completed and edited by Madame Vosmaer and Dr. G. P. Bidder.

The list of titles, the earliest of which is a work by Entzel, appearing in 1551, and the most recent by Zahalka, published in 1913, includes books and articles on recent as well as fossil sponges. Abstracts, translations, reviews, etc., with a few exceptions, have been excluded from the list. The bibliography is preceded by the author's preface as well as one by Dr. Bidder and is concluded by an index of the names of the authors given in the list. It is a valuable reference work for all those interested in sponges.

AFRICAN JUNGLE LIFE. *By A. Radclyffe Dugmore.* *The Macmillan Co.* $6.00 $7\frac{1}{4}$ x 10; viii + 246 *New York*

In recent years a number of books have appeared on animal life in the jungle in which the authors have more or less abandoned the method of describing their observations in a purely objective manner and have sought to convey to the reader an understanding of what existence for some of the "big game" animals really means from the animal view point. Such books are interesting when done by persons who have had long acquaintance with jungle animals. The present volume qualifies as one of the finest examples of its kind. The author, without obvious exaggeration, describes the pleasures and worries, the affections and fears, and the struggles to live of five types of animals—the elephant, the lion, the buffalo, the rhinoceros and the giraffe. The book is beautifully illustrated.

THE LEAFHOPPERS OF OHIO. *Ohio Biological Survey Bulletin 14 (Vol. III, No. 4).* *By Herbert Osborn.* *University Press* $1.00 *Columbus, O.* $6\frac{3}{4}$ x $9\frac{3}{4}$; 175 (paper)

Represents records accumulated for 30 years on the Cicadellidae of the State of Ohio, and includes some of the species which have not as yet been collected within the borders of the state, but which from their occurrence in adjacent states and in some cases from the Atlantic coast to the Mississippi River will no doubt be found when sought under the proper conditions. "The paper will therefore serve as a fairly complete survey for the group for the Ohio River valley or the territory from the Alleghenies to the Mississippi River and from Lake Erie to Tennessee."

There is an index to the genera and a short list of references.

EXPERIMENTAL STUDY OF THE FUNCTION OF THE OYSTER GILLS AND ITS BEARING ON THE PROBLEMS OF OYSTER CULTURE AND SANITARY CONTROL OF THE OYSTER INDUSTRY. *Bureau of Fisheries Document No. 1035.* *By Paul S. Galstoff.* *Government Printing Office* 15 cents *Washington, D. C.* $7\frac{1}{2}$ x 11; 39 (paper)

The author's investigations deal with the rate of flow produced by the oyster gills, with special reference to the effects of temperature; with the filtering action of the gills; and with the length of time the oyster shell is open. He finds that no current is produced at 5°C., and that the optimum temperature is between 25° and 30°. The gills filter out from 80 to 99 per cent of the plankton organisms. The average period during which the

oyster shell was open was 17 hours out of 24, with no correlation with the time of day.

IV. TERTIARY AND PLEISTOCENE MOLLUSCA FROM THE GALAPAGOS ISLANDS. V. LANDSHELLS OF THE GALAPAGOS ISLANDS. *Proceedings of the California Academy of Sciences. Fourth Series. Vol. XVII, Nos. 4 and 5.*
*By William H. Dall and Washington H. Ochsner.* *California Academy of Sciences*
75 cents *San Francisco*
$7\frac{3}{8}$ x 10; 96 + 8 plates (paper)

Both of the authors of this report are deceased. The contents are an edited presentation of an almost complete manuscript left by them, giving their findings during the 1905–1906 expedition from the California Academy of Sciences to the Galapagos Islands. Part IV deals with fossil Mollusca. Part V gives an introduction to geographical and meteorological conditions of the Islands, and an account of the landshells. There are a considerable number of photographic illustrations.

DIPTERA BRACHYCERA AND ATHERICERA OF THE FIJI ISLANDS. *Based on Material in the British Museum (Natural History).*
*By Mario Bezzi.*
*British Museum (Natural History)*
$5\frac{1}{2}$ x $8\frac{1}{2}$; viii + 220 *London*

The author of this volume, whose death occurred before its publication, found the dipterous fauna of Fiji to be "a typically endemic one of Austro-Malayan origin, with a small number of imported elements." From specimens forwarded to him by a number of collectors of Diptera of the Fiji Islands he was able to increase the number of species from the thirty already recorded to two hundred and thirty-nine. In the text of this volume are 54 figures. There is an index of families, genera and species.

THE MOSQUITOES OF THE AMERICAS. *Carnegie Institution of Washington Publication No. 387.*
*By Harrison G. Dyar.*
*Carnegie Institution of Washington*
$6.00 (cloth) *Washington, D. C.*
$5.00 (paper)
$6\frac{3}{4}$ x 10; 616

A detailed and exhaustive presentation of the taxonomy of the sub-family Culicinae of the family Culicidae of the order Diptera, as found in the Americas.

We note with regret the report of the recent death of the author at the age of 62. He was one of the foremost authorities on mosquitoes in our country.

FOOD OF BULLHEADS. *Bureau of Fisheries Document No. 1037.*
*By Louella E. Cable.*
*Government Printing Office*
5 cents *Washington, D. C.*
$5\frac{7}{8}$ x $9\frac{1}{8}$; 15 (paper)

The chief findings of this study are the following:

Bullheads prefer animal food in the form of insect larvae, pupae, and nymphs, crustaceans, bivalve mollusks, and snails, but are able to take other food in the absence of these.

Bullheads do not eat the eggs nor the young of other fish, except occasionally in very small amounts.

Juvenile bullheads eat virtually the same kinds of food as adults.

PHYSIOLOGUS. *A Metrical Bestiary of Twelve Chapters.*
*By Bishop Theobald (Translated by Alan W. Rendell). John and Edward Bumpus, Ltd.*
10 s. 6 d. *London*
$5\frac{1}{2}$ x $8\frac{1}{8}$; xxvi + 100

This is a beautifully printed new translation of Bishop Theobald's pious verses about animals. The text of the original edition is reproduced in facsimile. The translation is charming, and the very full commentaries and annotations furnish the background necessary to a complete appreciation of a noteworthy addition to the library of any biologist with antiquarian or theological tastes.

EINFÜHRUNG IN DIE TIERKUNDE.
*By Albert Fleischmann* *Gustav Fischer*
10.50 marks (paper) *Jena*
12 marks (cloth)
$6\frac{7}{8}$ x $10\frac{1}{4}$; viii + 228

This textbook is designed to cover the first semester's work in general zoology. It follows conventional lines, but commendably works in more embryology than corresponding American courses usually do. American teachers will get some pedagogical hints by looking it over. It is well illustrated and indexed.

A LABORATORY MANUAL OF INVERTEBRATE ZOOLOGY.
*Fourth Edition, Revised.*
*By Gilman A. Drew. With the aid of former and present members of the Zoological staff of instructors at the Marine Biological Laboratory, Woods Hole, Mass. W. B. Saunders Co.*
$2.25 *Philadelphia*
5 x $7\frac{5}{8}$; xiii + 234

A fourth edition of the manual used in courses at the Marine Biological Laboratory at Wood's Hole. It has been revised by the staff of the Laboratory so as to bring the classification, literature lists and nomenclature up to date. Also some of the directions for laboratory class work have been modified.

NORTH AMERICAN FAUNA No. 51. *A Taxonomic Review of the American Long-tailed Shrews (Genera Sorex and Microsorex).*
*By Hartley H. T. Jackson.*
*Government Printing Office*
50 cents *Washington, D. C.*
$5\frac{3}{4}$ x $9\frac{1}{8}$; 238 (paper)

A thorough and careful revision of the genera *Sorex* and *Microsorex*. The author recognizes 89 forms of 39 species. There are illustrations of skulls and teeth, a bibliography, and an index.

PRAIRIE BIRDS.
*By B. J. Hales.* *The Macmillan Co.*
$3.00 5 x $7\frac{1}{2}$; xv + 334 *New York*

Descriptions, with some remarks on their habits, of the birds of the Canadian prairies. A useful guide for the amateur.

THE ELASMOBRANCH FISHES.
*By J. Frank Daniel.*
*University of California Press*
$5.00 7 x $10\frac{1}{4}$; xi + 332 *Berkeley*

A second edition, somewhat enlarged by the addition of new material and

illustrations, of a standard zoological text.

## BOTANY

NORTH AMERICAN ORCHARDS. *Their Crops and Some of Their Problems.* *By William H. Chandler.* *Lea and Febiger* $4.50 5¼ x 7¾; 516 *Philadelphia*

A practical book for the orchardist. The author has an extensive acquaintance of the fruit growing industry in widely separated areas. That he sees clearly the problems and difficulties of those who make a business of fruit growing is indicated when he states that "the educated orchardist must base his judgements (diagnoses) in part upon such general scientific principles as we know, but usually in much larger part upon knowledge of many details and unexplained experiences." He points out that very often there must be uncertainty as to what is the best practice in orchard growing in spite of all that science has contributed to a knowledge of it. Not only must the orchardist be acquainted with the problems of climatic response, outstanding diseases, insect enemies, bearing habits and market qualities of the fruit of the varieties that he may grow, but he must likewise know what these problems are for his competitors in other sections of the country.

Notwithstanding the solidly written 500 pages, and the fact that the book is written primarily for the man who operates the orchard for a living, it is in no way formidable. Devoid of technicalities, the amateur will find it not only within his ken but interesting reading as well. At the end of each chapter there are lists of suggested reading for those who wish to study a particular subject more intensively. There is a detailed index.

PRINCIPLES OF PLANT PHYSIOLOGY. *By Oran Raber.* *The Macmillan Company* $3.00 5½ x 8½; 377 *New York*

A new textbook of plant physiology intended, so the author says with emphasis, for *students* and not for *teachers*. The material is well organized and well presented. In fact it is so good that we wish the author would now write an advanced textbook on the same subject. The chief criticism we are inclined to make of the book is that it seems a little out of balance. Out of a total of thirty-one chapters twenty-three deal with one or another aspect of metabolism; one with growth; and two with irritability and movement. Surely these three latter subjects deserve more space, even in an elementary text. We do not urge the cutting of the other parts, but the expansion of these. But, even as it stands, the book is an excellent one.

THE GASTEROMYCETES OF THE EASTERN UNITED STATES AND CANADA. *By William C. Coker and John N. Couch.* *The University of North Carolina Press* $12.00 *Chapel Hill* 7¾ x 10¾; ix + 201

A beautifully printed and exhaustive handbook of the Gasteromycetes. For its preparation all the available species were studied at first hand, including those at Persoon's herbarium at Leiden, Bresadola's at Stockholm, Kew Herbarium, New York Botanical Garden Herbarium, Curtis Herbarium, Schweinitz Herbarium,

Lloyd Herbarium, and the Pathological and Mycological Herbarium at Washington.

There are a large number of photographic plates, extensive bibliographical references, and an index. The University of North Carolina is to be congratulated on this splendid production.

A LABORATORY MANUAL OF GENERAL BOTANY.
*By Emma L. Fisk and Ruth M. Addoms.*
*The Macmillan Co.*
$1.00 5½ x 8½; ix + 103 *New York*

These exercises have been written "to accompany the Revised Edition of 'A Textbook of General Botany' by Smith, Overton, Gilbert, Denniston, Bryan and Allen, and in general a similar order of treatment has been observed." "The general plan of the course is to introduce the subject through a study of seed plants, and to use the facts and principles learned as a basis for a comparative study of the main groups of the plant Kingdom." The directions are clearly and simply presented, and there is a sufficient amount of brief explanatory text to make the immediate objectives intelligible without reference to outside sources.

FACTORS IN THE INCEPTION AND DEVELOPMENT OF FUSARIUM ROT IN STORED POTATOES. *United States Department of Agriculture Technical Bulletin No. 62.*
*By Freeman Weiss, J. I. Lauritzen and Philip Brierley.* *Government Printing Office*
15 cents. *Washington, D. C.*
5¾ x 9; 36 (paper)

Fusarium rot is responsible for a loss of from 5 to 10 per cent of the annual potato crop of the country. The present bulletin gives an account of experimental investigations of various factors of importance in the development of the rot, especially temperature, humidity, injury to the tuber, and differences in varieties of potato. Recommendations are given as to the treatment of potatoes to minimize loss from rot.

A TEXTBOOK OF GENERAL BOTANY.
*By Gilbert M. Smith, James B. Overton, Edward M. Gilbert, Rollin H. Denniston, George S. Bryan and Charles E. Allen.*
*The Macmillan Co.*
$3.75 5⅝ x 8½; x + 539 *New York*

A revised edition of this excellent text. The same plan and order of presentation as that of the original work is preserved here, but there has been a good deal of expansion in the treatment. Chapter XXXII on Evolution might better have been placed last, where it could be easily removed for an edition to be distributed in those states of our Bible Belt where biology is still studied.

PRINCIPLES OF PLANT PATHOLOGY.
*By Charles E. Owens.*
*John Wiley and Sons, Inc.*
$4.75 6 x 9; xii + 629 *New York*

An excellent general textbook of plant pathology for students in agricultural colleges. Part I deals with general topics, while Part II discusses in detail particular diseases, classified on an etiological basis. The book is thoroughly illustrated, documented, and indexed, and should take rank as a standard text in its field.

FIELD MANUAL OF THE FLORA OF OHIO AND ADJACENT TERRITORY.
*By John H. Schaffner.* *R. G. Adams and Co.*
$3.00 4½ x 6¾; 638 *Columbus, O.*

A pocket manual by means of which plants of Ohio and the adjacent territory can be identified from fresh material. In general the characters used are the flowers and vegetative parts present when the plant is in bloom. There is a glossary of common botanical terms and an index.

POLLENANALYTISCHE UNTERSUCHUNGEN AN SCHWEIZER-MOOREN UND IHRE FLORENGESCHICHTLICHE DEUTUNG. *Veröffentlichungen des Geobotanischen Institutes Rübel in Zürich. 5. Heft.*
*By Paul Keller.* *Hans Huber*
6⅜ x 9¼; 163 (paper) *Bern*

Detailed results of an investigation of the stratigraphy of Swiss peat bogs, carried out by an ingenious method, which depends upon the identification in the borings of the pollens of some ten species of forest trees.

## MORPHOLOGY

THE DEVELOPMENT OF THE HUMAN EYE.
*By Ida C. Mann.* *The Macmillan Co.*
$12.00 6¼ x 9¾; x + 306 *New York*

Certainly the most authoritative and comprehensive treatise in English on the embryology of the eye. Based on profound knowledge and extensive original research with an exceptionally complete series of human embryos, lucidly written, simply but clearly and profusely illustrated by the author, it is a work deserving of high praise. Both the general biologist interested in the subject as an aspect of ontogeny, and the ophthalmologist concerned with the origin of congenital eye defects will turn to it for reference.

A LABORATORY MANUAL FOR COMPARATIVE ANATOMY.
*By Malcolm E. Little and Rudolf T. Kempton.* *The Macmillan Co.*
$2.25 5½ x 8½; xix + 286 *New York*

A new laboratory guide in vertebrate comparative anatomy, planned to steer a compromise course between the Huxleyan method of studying types exclusively, and the more recent pedagogic technique of focussing attention upon organ systems. The material is well arranged for teaching purposes.

## PHYSIOLOGY AND PATHOLOGY

LABORATORY DIAGNOSIS AND EXPERIMENTAL METHODS IN TUBERCULOSIS.
*By Henry S. Willis (With a Chapter on Tuberculo-Complement Fixation, by J. Stanley Woolley, and Introduction by Allen K. Krause).*
Cloth: $3.50 *Charles C. Thomas*
Keratol: $4.25 *Springfield, Ill.*
6 x 8¾; xxv + 330

The multifarious aspects of tuberculosis have assumed such large dimensions and become so complicated with detail that it requires expert and long study to become thoroughly acquainted with even individual phases. The author of this volume is eminently qualified in this respect to deal with the subject in hand. He has for many years been associated with the Kenneth Dows Research Laboratories for the study of tuberculosis at the Johns

Hopkins Hospital, and has had opportunity to deal critically and at first hand with all the laboratory methods that pertain to the study and treatment of tuberculosis.

The work comprises five parts: I. General considerations of the body fluids and excreta; II. Bacteriological diagnosis; III. Diagnosis by use of tuberculin; IV. Serological diagnosis; V. Some methods of value in studies of tuberculosis experimentally produced. It is clearly written, with many illustrations, provided with detailed practical directions, a long bibliography, and an index. The book should be in every laboratory concerned in any way with tuberculosis, and consulted by every student who expects to meet the disease as a practical problem.

THE RESPIRATORY FUNCTION OF THE BLOOD. *Part II: Hæmoglobin.*
*By Joseph Barcroft.* *The Macmillan Co.*
$5.00 $6\frac{1}{8}$ x $9\frac{3}{4}$; ix + 200 *New York*

The classical studies of Barcroft recorded in his *Respiratory Functions of the Blood*, printed in 1913, are to be reissued and brought up to date in a series of separate volumes dealing with different phases of the subject. The first volume, *Lessons from High Altitudes*, appeared in 1925. This is the second and deals with what L. J. Henderson has characterized as the second most interesting substance in the world, hæmoglobin.

In it Barcroft takes up the chemistry of hæmoglobin and its constituent elements, its distribution among species, the statics and dynamics of its combination with oxygen and other gases, its solution properties, and the effect of temperature on it. There is a closing discussion of the biological significance of the substance.

The book is, as is to be expected, well written, in intimate contact with the history of the subject and the personalities who contributed to its development.

There is an index and references are appended to each separate chapter, but there is no general bibliography.

DIE PHYSIOLOGIE DER THYMUS.
*By Frederick S. Hammett.*
*Urban und Schwarzenberg*
2.50 marks *Berlin*
7 x 10; 22 (paper)

This little essay is in the series *Fortschritte der Naturwissenschaftlichen Forschung*, edited by Dr. Emil Abderhalden. The author considers the subject didactically under the following heads: Growth of the Thymus; Autolysis of the Thymus with Age; Factors of Internal Secretion associated with Involution of the Thymus; Feeding and Extirpation Experiments; Physiological Effects of Thymus Extracts; The Function of the Thymus. A good measure of what is presented comes from his own work. He concludes "The function of the thymus is not yet clear."

EXERCITATIO ANATOMICA DE MOTU CORDIS ET SANGUINIS IN ANIMALIBUS.
*By William Harvey (With an English Translation and Annotations by Chauncey D. Leake).* *Charles C. Thomas*
$3.50 *Springfield, Ill.*
$6\frac{1}{4}$ x $9\frac{1}{4}$; 154

A new translation of the *De Motu Cordis*, with some useful annotations. The volume also contains a facsimile of the 1628 edition, and a chronology of Harvey's life. The translation is good, and will probably be found easier reading than the original English translation of 1653, and

certainly easier than Willis's translation of 1847. The publisher has attempted to produce a volume which will be a worthy memorial to the tercentenary of the original publication. There is a good index.

THE BLOOD PLASMA IN HEALTH AND DISEASE.

*By J. W. Pickering.* *The Macmillan Co.*
$4.25 5½ x 8½; xi + 247 *New York*

Specialization grows apace. A book on blood covers too wide a range. So now we have in this volume an excellent text book devoted to the *plasma* of the blood only. Successive chapters deal with the protein of the plasma; fibrinogen; the inception of clotting; stabilization of plasma; thrombins and antithrombins; fibrin; suppression of coagulability *in vivo*; the blood in anaphylaxis; theories of coagulation; arrest of hemorrhage; thrombosis; menstrual and puerperal blood; and the blood of bleeders. There is a bibliography of some seventeen closely printed pages, and a detailed index. This is a useful addition to the literature.

LABORATORY EXPERIMENTS IN PHYSIOLOGY.

*By W. D. Zoethout.* *The C. V. Mosby Co.*
$2.25 6 x 9; 251 *St. Louis*

While this laboratory guide was planned to accompany the author's textbook, it is so arranged that any other textbook will serve about as well. As it is intended for the student whose time for the subject is somewhat limited, it is not burdened with unnecessary matter. "Preparation" questions prefacing each experiment are to be studied before going to the laboratory. All kymographic records and coordinate graphs have been omitted, the author considering these to have no place within a laboratory manual.

A TEXTBOOK OF BACTERIOLOGY.

*A Treatise on the Application of Bacteriology and Immunology to the Etiology, Diagnosis, Specific Therapy and Prevention of Infectious Diseases for Students and Practitioners of Medicine and Public Health.*

*By Hans Zinsser (with a section on Pathogenic Protozoa by E. E. Tyzzer).*

*D. Appleton and Co.*
$7.50 6¼ x 9¼; xx + 1053 *New York*

In this sixth edition, the entire contents of the leading American textbook of bacteriology has been revised, bringing all chapters up to date. The original purpose of developing the book into a manual of infectious diseases has been adhered to, so that it still maintains its importance for physicians and health officers, as well as for undergraduate students of medicine.

THÉORIE IONIQUE DE L'EXCITATION DES TISSUS VIVANTS.

*By P. Lasareff.* *Albert Blanchard*
40 francs 6½ x 10; 240 (paper) *Paris*

An attempt to establish quantitative laws of sensation (taste, smell, etc.), largely through mathematical methods of reasoning and analysis, upon a physicochemical observational base. The book summarizes the results of the work done in the author's laboratory during the past quarter of a century. Dr. Lasareff is Director of the Institute of Physics and Biophysics at Moscow.

CANCER AND CANCER RESEARCH. *A Series of Articles for the Lay Public. Compiled by a Scientific Committee of the Liverpool Medical Research Organization.* *Sherratt and Hughes*
1 s. 6 d. *Manchester*
$5\frac{1}{2}$ x $8\frac{1}{2}$; 75 (paper)

This is a reprint of a series of articles on various phases of the cancer problem compiled for the lay public by a scientific committee of the Liverpool Medical Research Organization. These appeared first in the Liverpool Daily Post and Mercury for March, April and May, 1928.

A TEXTBOOK OF PHYSIOLOGY.
*By W. D. Zoethout.* *The C. V. Mosby Co.*
$4.50 6 x 9; 664 *St. Louis*

The third edition of a book which was especially planned for students in dental, pharmacy and normal schools where the time devoted to physiology is too limited to make advisable the use of any of the larger works as a text. This edition has been throughly revised, many topics added or expanded, while less important subjects have been dropped.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *In 75 Vorlesungen für Studierende, Ärzte, Biologen und Chemiker. II Band: Stoffwechsellehre. VI (Schluss-) Lieferung: Purin und Kohlehydratstoffwechsel, Vorlesung: LXIII bis LXXV.*
*By Otto Fürth.* *F. C. W. Vogel*
15 marks *Leipzig*
7 x 10; vi + 280 (paper)

This fascicle completes the second volume of this new edition of a standard text, of which earlier parts have been noticed in THE QUARTERLY REVIEW OF BIOLOGY. It deals with purine and carbohydrate metabolism.

HUMAN PHYSIOLOGY. *A Text-Book for High Schools and Colleges. Fifth Edition Revised.*
*By Percy G. Stiles.* *W. B. Saunders Co.*
$2.25 5 x $7\frac{3}{4}$; 444 *Philadelphia*

A fifth edition of Professor Stiles' well known text book. It is well adapted for high schools, but there are some uplifting passages which do not add materially to its value.

TIERPHYSIOLOGISCHES PRAKTIKUM *für Studierende der Landwirtschaft und Veterinärmedizin.*
*By E. Mangold.* *Julius Springer*
3 marks $5\frac{3}{8}$ x $8\frac{1}{4}$; 53 (paper) *Berlin*

Laboratory directions for a year's course in animal physiology, with two laboratory periods per week.

## BIOCHEMISTRY

THE PROTAMINES AND HISTONES. *By A. Kossel (Translated by W. V. Thorpe).* *Longmans, Green and Co.*
$3.25 6 x $9\frac{1}{2}$; xi + 107 *New York*

The group of substances comprising the subject matter of this work is of a rather specialized interest, and their study does not come under the purview of the general chemist's work. It is all the more fortunate therefore that the extensive investigation of them by the author was rescued for science before his death, and presented in this easily available form to English readers.

The protamines and histones are proteins

characterized by their basic reaction, as distinguished from the acid reaction of the more widely distributed proteins, the protamines being in addition specially noteworthy for their simplicity of structure. Of particular interest to the biologist is their association with the nuclear portion of the cell, and their biological distribution, the protamines being limited to the sperm of certain fish, and the histones to the germ plasm of some vertebrates and invertebrates, the red cells of birds and the thymus gland of certain mammals.

There is a long bibliography and an index.

THE DETERMINATION OF HYDROGEN IONS. *An Elementary Treatise on Electrode, Indicator and Supplementary Methods with an Indexed Bibliography on Applications.*
*By W. Mansfield Clark.*
*The Williams & Wilkins Co.*
$6.50 6 x 9; xvi + 717 *Baltimore*

The third edition of this standard treatise has been greatly, indeed almost completely, rewritten. The total pages have increased from 480 to 717 (49 per cent increase); the subject index covers 51 per cent more space, and the author index covers 154 per cent more space. The bibliography on applications has been completely revised, and now consists of some 1600 titles, of which only about 600 were included in the second edition.

Those interested in growth curves may well glance at the diagram on page x, showing the number of papers dealing with pH measurements published each year from 1911 to 1927; in the latter year the total was over 1450.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 272.* Containing following articles: *Methodik der Gewebselastometrie und der H-Ionenmessung am lebenden Organismus*, by Heinrich Schade and Karl Mayr; *Die polarographische Methode*, by Silvester Prát; *Die Pufferlösungen bei der colorimetrischen Bestimmung der Wasserstoffionen-konzentration*, by I. M. Kolthoff; *Methodik der Bestimmung der Capillarität*, by Karl Schultze.
*Urban und Schwarzenberg*
9 marks 7 x 10; 172 (paper) *Berlin*
*Lieferung 283.* Containing following articles: *Die quantitative Spektralanalyse*, by M. C. Keller; *Die Verwendung des Schmalfilms für biologische Zwecke*, by W. R. Hess; *Farbmessungen an gefärbten Körperflüssigkeiten mit dem Pulfrichschen Stufenphotometer*, by Ludwig Heilmeyer.
*Urban und Schwarzenberg*
6 marks 7 x 10; 104 (paper) *Berlin*
*Lieferung 284. Photographische Absorptionsspektrophotometrie.*
*By Günther Scheibe.*
*Urban und Schwarzenberg*
3 marks 7 x 10; 50 (paper) *Berlin*

These three numbers in the great Abderhalden handbook are of primary interest to biochemists and biophysicists. They impress one once more with the thoroughness and comprehensiveness of this colossal undertaking.

DIE METHODIK DER FERMENTE. *Lieferungen II und III.*
*Edited by Carl Oppenheimer and Ludwig Pincussen.* *Georg Thieme*
*Leipzig*
Lief. II, 28 marks
$7\frac{3}{4}$ x $10\frac{1}{2}$; vii + 304 (paper)
Lief. III, 28 marks 944 (paper)

Part I of this work, which is projected

as a comprehensive treatise on ferments, was noted in this REVIEW (Vol. III, No. 3, 452–3). Parts II and III follow the general arrangement there described, i.e., various general divisions of the subject are taken up independently by different authors. Part II continues the consideration of substrates begun in I and contains a division *C* devoted to the obtaining and purification of ferments. Part III begins the second main division, which includes chapters on the esterases, diastases, nucleoses, urease, and arginase.

COLLOID CHEMISTRY.
*By The Svedberg in collaboration with Arne Tiselius.* *Chemical Catalog Co., Inc.*
$5.50 5¾ x 9; 302 *New York*

The second edition of a standard introductory treatise to the subject of the physics and chemistry of colloids. The work has been thoroughly revised and enlarged in this edition, more attention in particular being paid to X-ray analysis of the structure of sols and gels, Donnan potentials, the technique of ultramicroscopy, and the measurement of diffusion and cataphoresis.

RECENT ADVANCES IN CHEMISTRY IN RELATION TO MEDICAL PRACTICE.
*By W. McKim Marriott.*
*The C. V. Mosby Co.*
$2.50 6 x 9; 141 *St. Louis*

A series of six lectures before the San Diego Academy of Medicine in 1927. The subjects were: fundamental chemical considerations; acidosis and alkalosis; chemistry of the blood; food and metabolism; and endocrines.

APPLIED BIOCHEMISTRY.
*By Withrow Morse. Revised and reset with the coöperation of Joseph M. Looney.*
*W. B. Saunders Co.*
$7.00 5¾ x 9¼; 988 *Philadelphia*

The first edition was noticed in THE QUARTERLY REVIEW OF BIOLOGY, Vol. 1, No. 3. There is nothing to add to what was there said, except that the subject is again brought up to date, eighteen months having elapsed between the writing of the first and second editions.

## SEX

THE CONQUEST OF LIFE.
*By Serge Voronoff (Translated by G. Gibier Rambaud).* *Brentano's*
$3.50 5½ x 8⅛; 201 *New York*

This is a translation of Dr. Voronoff's *La Conquête de la Vie*, which was reviewed here in September, 1928. There is little to add to what was then said. We feel obliged, however, to call attention to this passage: "Abélard, the brilliant poet, never wrote a line after he was emasculated, by the orders of the cruel uncle of Héloïse, at the age of forty." The French text shows that "line" here means "line of poetry"; but whether the fact is an indication of Abélard's diminished intellectual powers (as the author implies) seems doubtful. In point of fact, Abélard wrote a good deal after his operation, but it was theology and not love poetry.

SOME MORE MEDICAL VIEWS OF BIRTH CONTROL.
*Edited by Norman Haire.*
*E. P. Dutton and Co., Inc.*
$2.50 5 x 7⅜; x + 216 *New York*

The purpose of this treatise is frankly

propagandist. It is a collection of eleven essays dedicated to Margaret Sanger. All discussion of contraceptive technique is omitted in deference to American laws. We wish that Professor F. A. E. Crew had not lent his name and his pen to this book. To be sure his essay is the best in the lot, as would be expected. But his remarkable talents both as writer and as investigator surely deserve to be put to better uses than bolstering up the respectability of a book like this.

## BIOMETRY

F. Y. EDGEWORTH'S CONTRIBUTIONS TO MATHEMATICAL STATISTICS.

*By A. L. Bowley. Royal Statistical Society*
5 shillings *London*
5½ x 8½; vii + 139 (paper)

Professor Bowley has rendered an important service to mathematical statisticians in this monograph. He has collected and rewritten all of Edgeworth's most important work in statistical theory —no light task. Edgeworth's own papers are by no means easy reading, and not the least of Professor Bowley's services has been to clarify and amplify points which the original papers left obscure.

Whether Edgeworth's work is of great value to the practical statistician seems to us rather doubtful; but we can recommend it to the statistician who is interested in the mathematical philosophy behind his work—not because he ought to agree with all of it, but because it is worth thinking about.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 265.* Containing the following articles: *Die Methodik biometrischer Messungen an Laboratoriumsversuchstieren*, by Karl Saller; *Rassenpathologische Methoden*, by Albert Plehn; *Zur Technik der Injektion der Lymphgefässe*, by Hermann Baum.

*Urban und Schwarzenberg*
9 marks 7 x 10; 182 (paper) *Berlin*

The bulk of this number of the Abderhalden handbook is devoted to an extremely valuable discussion of the application of modern, refined, anthropometric and osteometric technique to the smaller laboratory mammals. It is a welcome addition to the literature.

## PSYCHOLOGY AND BEHAVIOR

EXPLORING YOUR MIND *with the Psychologists.*

*By Albert E. Wiggam. The Bobbs-Merrill Co.*
$3.50 5¾ x 8¾; 419 *Indianapolis*

Mr. Wiggam has taken on himself the Huxleyan task of bringing scientists and their works to the layman. Some of the eminent figures of the laboratories who have been thus prominently exposed to the public eye are pleased with the results, others not. We are under the general impression that the "nays" have it.

Hitherto our author has been mostly occupied with genetics and eugenics, and biologists have come in for most of his notice. He now turns his active pen on the psychologists. Having interviewed a number of them, he reports here his impression of their teachings, as gleaned from conversation. The following are represented, *in person* by good portraits, and by excerpts from their remarks: Professor Edward Lee Thorndike, Dr. Donald A. Laird, Prof. Henry Foster Adams, Dr. David Mitchell, Prof. Lewis Madison Terman, Dr. Catherine Cox Miles,

Prof. Carl Emil Seashore, Dr. J. McKeen Cattell, Dr. Mark A. May, Dr. Hugh Hartshorne, Dr. Michael I. Pupin.

What Mr. Wiggam understands of the purpose of science may be gathered from two quotations taken from either end of his work.

> In fact, I do not think it does people very much good to learn the marvels of the atom or the germ-cell unless at the same time they are taught how to make this knowledge helpful for solving their daily problems, inspiring for their hours of meditation, consoling in their days of grief, enlightening in their periods of doubt, heartening in their moments of fear, exalting in their times of triumph and success.

And in the *finale* by Michael Pupin, (the eminent electrician somehow gets into this group of psychologists):

> Science is making us better Christians.
>
> Science is teaching men how to cooperate intelligently with God; it is teaching men what His laws are and how to obey them.
>
> Science is proving that the human soul is the greatest thing in the Universe, the supreme purpose of the Creator.
>
> Science is leading us closer and closer to God.

We might be moved to enter a vigorous protest against the intrusion of this sort of evangelism into scientific discussion, but we cannot when Mr. Wiggam is concerned. He writes too entertainingly and good naturedly to bear earnest opposition. He is very effective with the public, and his intentions are the best. Futhermore he is the sort that would be bound to be improving the world one way or another. If science didn't seduce him some other enthusiasm would—and we can think of worse.

THE SYMBOLIC PROCESS AND ITS INTEGRATION IN CHILDREN. *A Study in Social Psychology.* *By John F. Markey.* *Harcourt, Brace and Co.* $3.50 5½ x 8½; xii + 192 *New York*

This book is an attempt to explain the nature and development of language in the child. The author emphasizes particularly the importance of the social processes in the development of the "symbolic process" (which we take to be a high-toned name for language). With some of his statistical analysis we find it hard to agree; we doubt, for example, that he could give any justification for his calculation of a correlation coefficient on page 58. What he has actually done is calculate the correlation between the mean $y$ in an array and the corresponding $x$ for the array; which not unnaturally (since the arrays contain 100 individuals each) gives him a correlation coefficient of $-.975$. Actually, of course, the coefficient will be much less than this, but as we are given no information about the scatter in the arrays it is impossible to say what its value would be.

The book is exceedingly difficult reading. We recommend to Dr. Markey that he meditate upon the literary style of Bertrand Russell, who somehow manages to make subjects of far greater intrinsic difficulty seem much simpler than anything in the present volume.

JUDGMENT AND REASONING IN THE CHILD. *By Jean Piaget (In collaboration with Mlles. E. Cartalis, S. Escher, A. Hanhart, L. Hahnloser, O. Matthes, S. Perret and M. Roud).* *Harcourt, Brace and Co.* $3.75 5⅝ x 7½; viii + 260 *New York*

Piaget is still a young man, but he has already achieved two notable essays on the psychology of childhood. In *Language and Thought in the Child* he advanced the thesis that thought in the early

years is essentially egocentric, i.e., its aim is self satisfaction, and it has not yet felt the obligation to be acceptable to others. In this volume he traces its growth through the ages 11–12 years.

The key to his theory is that the development of thought takes place in the direction of a greater sense of its social responsibility. Logicality arises from the need to have our thoughts carry conviction with others; in the child up to 7–8 years, when ego-centrism is dominant, this quality is absent. Instead it has "juxtaposition" and "syncretism." Juxtaposition is the tendency to juxtapose objects seen together, with no sense of their relation to a synthetic whole, as when a child draws a bicycle by inserting all the parts but not in any functional relation, one to the other. Syncretism is the complementary tendency of seeing the whole in an undifferentiated fusion with no recognition of the relation to it of the constituent elements. After 7–8 years there is a diminution of egocentrism and with this, hand in hand, a development of logicality. The child is able to achieve, though only in a limited way at first, the viewpoint of other individuals, his friends; but not yet the objective outlook that comes with placing oneself in the disposition of inanimate objects. Syncretism, juxtaposition, inability to handle relationships, etc., are still discernable in his thought, but they are shifted to the language plane; in the sphere of action there has been progress from these characters. Accordingly thought characteristically reverts to experience; where hypothetical questions are involved, the child's mind at this stage fails. It is not till 11–12 years that the mind becomes sufficiently liberal in a willingness to separate itself from the ego, to attain the viewpoint of abstract relationship, and the formal reasoning of the adult begins.

So much for the theory in rather inadequate general outline. In support of it the author elicits his analysis of experiments with the use by children of conjunctions expressing causal, logical and discordant relations, their response to the Binet Simon tests by absurd phrases, as well as the logical content of their spontaneous conversation. The experience dealt with is admittedly not large but in good accord with the author's general thesis. The obvious objection to results obtained from an examination of verbal characters, that they may be reflective of the accretion of information and the development of language rather than a change in the character of thought, the author fully appreciates. As regards the possession of requisite information, the simplicity and familiarity of the matters referred to in the tests is appealed to and as respects the acquisition of language, the author holds that the ability to express ideas is precisely the development which marks progress in logical thought.

The study will undoubtedly be welcomed as a support to the school of psychologists who hold to the instrumental, social function of thought, as represented in this country by John Dewey, particularly in his *Experimental Logic*. Like all psychological tracts which it is our fortune to encounter, it seems excessively verbose, and the shuttle movement of the argument, with repeated recourse to points already established makes it heavy reading. It is, however, well translated. There is an index, which helped us not at all to locate several items contained repeatedly in the text.

THE MODERN CAT: HER MIND AND MANNERS. *An Introduction to Comparative Psychology.*
*By Georgina S. Gates.* *The Macmillan Co.* $2.00 $5\frac{1}{4}$ x $7\frac{7}{8}$; xi + 196 *New York*

In this entertaining book the author, an assistant professor of psychology of Barnard College, discusses in simple and non-technical language what is known of the mind of the greatest of all household pets. The book is mainly a compilation of well known data, written for two classes of readers: "those who love cats and would like to know more about the explanation for their actions, and those who may wish to obtain, through a

description of methods employed with one animal, a first glimpse of the ways of comparative psychology."

Many popular beliefs concerning cat behavior are shattered. Much interesting and sound information is given which makes the cat appear to the average reader in a wholly new light. According to the author the cat, while possessing color vision, perceives only shades of gray. "She lives in a visual world much like ours at twilight," also "in an auditory world like that of the tone-deaf individual." Feeding experiments seemed to indicate that there was complete understanding between the cat and the experimenter when with a clapping of hands the words "I must feed those cats" were uttered and food was to be secured for the searching. However, the words "My name is Thorndike" were just as magical in stimulating the cat to search for its food, if uttered a sufficient number of times under the right conditions.

The title of the book is misleading in that there is the suggestion that the cat of today is somehow different from the cat of the past. There are four illustrations and several diagrams showing time curves in trial experiments for both cats and students. A list of the chief references consulted in preparing the book is given, and there is an index.

THE FUNDAMENTALS OF HUMAN MOTIVATION.
*By Leonard T. Troland.*
*C. Van Nostrand Co.*
$5.00 5½ x 8½; xiv + 521 *New York*

Hedonism translated into psychophysical terms. Nociceptive afferent nerve currents—those indicating injurious conditions—are accompanied by a decrease in conductance of the cortical adjustors and consequently by a change in the motor response; beneceptive currents—those indicating favorable conditions—are accompanied by an increase in conductance and a consequent enhancing of the motor response. Troland calls this change of conductance retroflex action, and bridges the psychophysical gap by the postulate that the affective intensity is proportional to the rate of change of conductance. On the basis of these principles he discusses, among other things, the pleasures of novelty, "the nature and foundations of emotional experience, the explanation of typical modern interests: automobiles, radio, and the like," and finally, "suggestions towards a scientific treatment of the problems of ethics." The book is well documented and contains a glossary and an index.

POLITICAL BEHAVIOR. *The Heretofore Unwritten Laws, Customs and Principles of Politics as Practiced in the United States.*
*By Frank R. Kent. William Morrow and Co.*
$2.50 5 x 7½; ix + 342 *New York*

All students of human biology should read this entertaining treatise by the leading political writer for the newspapers of these times and parts. It is replete with sound political information as well as realistic philosophy. It is not a book for old ladies of either sex. In fact Mr. Kent says that he

> is fully aware that some of the views herein expressed will likely be resented by those who have, in the words of the politicians of every generation, "an abiding faith in the fundamental intelligence of the American people." The natural tendency of these will be to insist that the opinions here given are warped or soured; that actually the caliber and character of the voters is not as depressingly low as here depicted; that a "broad view" will prove the people to have a real capacity for getting at the truth; that

in the "long run" they can be depended upon to act wisely and righteously. The answer is that it would be pleasant to think so, that perhaps it is a good thing to keep up the pretense, that there is of course a small minority of whom it is so. But so far as the vast majority is concerned the evidence is overwhelmingly against it and every clear-headed person who knows from personal contact the types composing the great bulk of the voters, knows it is not so of them.

HUMAN BEHAVIOR.
*By Walter S. Hunter.*
*The University of Chicago Press*
$2.00 5¼ x 8¼; 355 *Chicago*

FUNDAMENTALS OF OBJECTIVE PSYCHOLOGY.
*By John F. Dashiell. Houghton Mifflin Co.*
$3.00 5⅜ x 8; xviii + 588 *Boston*

These two text books cover practically identical ground, though the arrangement is somewhat different. On the whole we prefer Dr. Hunter's, as being shorter, somewhat better arranged, and rather more attractively printed (though neither stands out as a piece of book-making). Both books take an extreme behaviorist position, though Dashiell is broad-minded enough to admit in his preface that an introspective approach has occasional value.

It is interesting to note that both authors reproduce a part of Goddard's pedigree of the Kallikak family, and express no dissent from his view that feeble-mindedness is a Mendelian recessive.

PSYCHOLOGIE DES ANIMAUX.
*By F. Buytendijk (French translation by H. R. Bredo).* *Payot*
25 francs 5½ x 9; 315 (paper) *Paris*

An excellent review, interestingly written, of the present state of knowledge and opinion about animal behavior. The author exhibits real insight into animal psychology, a quality missing in the writings of some workers in the field of animal behavior, whose striving for complete objectivity results in nothing more important than complete heuristic sterility. We agree with Professor Claparède, who says in introducing the book that it ought to be read by all psychologists, veterinarians, breeders, hunters, trainers, horsemen, and lovers of animals generally, on the ground that it will teach them how better to appreciate animals.

THE PSYCHOLOGY OF INDIVIDUAL DIFFERENCES.
*By Robert S. Ellis. D. Appleton and Co.*
$3.50 5¼ x 8; xxiv + 533 *New York*

Covers the whole range of matters concerned with the question of psychological differences, in the typical manner of text book condensation. As merely ancillary to the treatment of the main topic, are taken up in successive chapters such subjects as the relation between body and mind, the analysis of the individual, statistical methodology, mental measurements, heredity. All the ideas are categorically labelled in the 523 pages contained in the book, about 1.8 ideas per page on the average. There is an index.

MOTIVE FORCES OF THE MIND.
*By Alice Raven. W. Heffer and Sons, Ltd.*
3 s. 6 d. net 5 x 7¼; vii + 94 *London*

This is a brief, well written account of the dynamic aspects of modern psychology, written primarily for an audience of women, chiefly settlement workers in East London. The point of view, and the

sources drawn upon, are mainly British. The discussion is sound and well balanced.

The book will be useful to the busy worker in other fields of science, who wishes, in an hour or two of reading, to gain some idea of what psychology has to say today regarding the practical working of the minds of themselves and of other people. There is no index.

HOW ANIMALS FIND THEIR WAY ABOUT. *A Study of Distant Orientation and Place-Recognition.*
*By Étienne Rabaud. Translated by I. H. Myers.* *Harcourt, Brace and Co.*
$2.75 5⅜ x 8½; 142 *New York*

A review of the literature regarding orientation in animals which comes to the conclusion that nothing more than the ordinary sense and motor organs of the body are required to account reasonably for the known facts. Chapters are devoted to orientation in flying and walking insects respectively; in other invertebrates; and in vertebrates. The book contains a bibliography of 71 titles, and an index, but not much new.

THE PROBLEM OF LAY-ANALYSES.
*By Sigmund Freud.* *Brentano's*
$2.50 5 x 7½; 316 *New York*

A consideration of at least some slight weight that would appear to bear against Freud's doctrine of the all-importance of the sexual interest for individual psychology is provided in his autobiographical sketch given in the latter half of this book. At only one point in the author's career when he *hurriedly* finished off a beginning work on cocaine in order to visit his fiancée, the sexual impulse seems to have been in the ascendant; otherwise his life appears to have been a steady drive of the scientific intellect. Always brilliant, he early made a reputation as a diagnostician and had achieved notable work in the field of neuropathology before his interest became focussed on psychiatry. After an initial period with Charcot and Janet, he tells of the gradual evolution of the body of ideas that are now well known under the name of psychoanalysis, and reveals a mind of great originality and tremendous courage. As to the enduring validity of his theories there may be much doubt, but at the very least he has taken psychopathology out of its academic ruts and given it dynamic quality.

The first part of the book is devoted to an advocacy of the participation by properly prepared laymen and women in the practice of psychoanalysis. The argument is presented in Socratic manner, as a conversation with a hypothetical Referee. It is not convincing.

## DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

SCEPTICAL ESSAYS.
*By Bertrand Russell.*
*W. W. Norton and Co., Inc.*
$2.50 5⅝ x 8⅜; 256 *New York*

This is an enormously entertaining book about a variety of subjects. Few if any living persons are so nimble of wit as its distinguished author. Nobody has to agree with him to enjoy the book. But if censors had sense they would suppress it at once, because a book more subversive of all that upright, good, forward looking Methodists and Baptists and Presbyterians are pleased to look upon as sound spiritual values was never printed. How stupid censors are! They will throw to the wolves a book that hasn't an idea in it,

good or bad, if it contains once a word of four letters that every child knows and is wholly undisturbed by. On the other hand a book like this one, which contains no such word, may circulate freely, regardless of the fact that it will permanently and incurably poison the mind of any young man or woman who reads it.

Take for example the essay on "Good Men."

> We all know what we mean by a "good" man. The ideally good man does not drink or smoke, avoids bad language, converses in the presence of men exactly as he would if there were ladies present, attends church regularly, and holds the correct opinions on all subjects. He has a wholesome horror of wrongdoing, and realizes that it is our painful duty to castigate Sin. He has a still greater horror of wrong thinking, and considers it the business of the authorities to safeguard the young against those who question the wisdom of the views generally accepted by middle-aged successful citizens. Apart from his professional duties, at which he is assiduous, he spends much time in good works: he may encourage patriotism and military training; he may promote industry, sobriety, and virtue among wage-earners and their children by seeing to it that failures in these respects receive due punishment; he may be a trustee of a university and prevent an ill-judged respect for learning from allowing the employment of professors with subversive ideas. Above all, of course, his "morals," in the narrow sense, must be irreproachable.

Having so accurately defined a "good" man Russell presently proceeds to discuss his usefulness. For example:

> Another of the uses of good men is that any undesirables can be kept out of politics by means of scandals. Ninety men out of a hundred commit breaches of the moral law, but in general this fact does not become public. And when in the ninety-ninth case it becomes known in relation to any individual, the one man in the hundred who is genuinely innocent expresses genuine horror, while the other ninety-eight are compelled to follow suit for fear of being suspected. When, therefore, any man of obnoxious opinions ventures into politics, it is only necessary for those who have the preservation of our ancient institutions at heart to keep track of his private activities until they discover something which, if exposed, will ruin his political career. They then have three courses open to them: to make the facts known and cause him to disappear in a cloud of obloquy; or to compel him to retire into private life by threats of exposure; or to derive for themselves a comfortable income by means of blackmail. Of these three courses the first two protect the public, while the third protects those who protect the public. All three, therefore, are to be commended, and all three are only rendered possible through the existence of good men.

HISTORY OF THE SHEFFIELD SCIENTIFIC SCHOOL OF YALE UNIVERSITY. 1846–1922. *Vols. I and II.*
*By Russell H. Chittenden.*
*Yale University Press*
$10 for two volumes *New Haven*
$6\frac{1}{2}$ x $9\frac{3}{4}$; xix + 610

In preparing the material for these two beautifully printed and illustrated volumes Professor Chittenden has performed a notable service for the history of science in America. Yale University and its Sheffield Scientific School have played an important rôle in the development of science, and particularly of technical education in this country.

The Sheffield Scientific School has a separate board of trustees, and separate endowment funds. Certain difficulties between the University and the School have arisen, apparently as a result of entirely natural processes, which Professor Chittenden fully describes. It does seem a pity, however, that such a fine record of important achievement should end on the following note: "What the future of the Sheffield Scientific School is to be depends largely upon the attitude of the Corporation of the University. Under the conditions now imposed the future looks dark. But what will be the verdict of thoughtful people upon a line of action which results in the dissolution of a once

progressive and powerful institution, a part of Yale University, of which there was much to be proud? Will memory of the accomplishments of the past be the only remainder of a school of science that played so important a part in the development of scientific education and scientific research in this country, from the middle of the nineteenth century on?"

A SHORT HISTORY OF MEDICINE. *Introducing Medical Principles to Students and Non-Medical Readers.*
*By Charles Singer. Oxford University Press*
$3.00 $5\frac{3}{8}$ x 8; xxiv + 368 *New York*

For wide scope of interest, deep learning and original research, the author of this little book stands foremost among historians of science writing in English. His continued devotion to writing for the general public is to be gratefully welcomed. The great cultural value of the history of science is still insufficiently appreciated. Skepticism of finality in thought and toleration of differences of opinion stand out as the moving forces in the history of scientific progress, and these qualities were never more needed in our policy than now.

Far from being a dry compendium of historical names and dates, the book emphasizes what the author calls the philosophy of medicine, by which he means its underlying principles rather than details of practical application. He traces the development of medical thought from the Greek period through modern times. Notable is the large proportion of space he devotes to recent history, more than half of the book being given over to modern medicine. The book is generously illustrated and has a good index.

THE GRAPHIC BIBLE *from Genesis to Revelation in Animated Maps and Charts.*
*By Lewis Browne. The Macmillan Co.*
$2.50 8 x $10\frac{3}{8}$; 160 *New York*

The talented author of *This Believing World*, noted in these columns earlier, has again put us in his debt by condensing the essence of the Bible as a narrative into a space of 160 pages, with an illustration from his own gifted hand on nearly every page. These illustrations are chiefly maps, which somehow convey a sense of reality as to place and time which we venture to think is sadly lacking in most biologists' knowledge of the events discussed in the Bible. Therefore we strongly commend this book to their attention. Aside from its great practical usefulness it is entertaining.

A POCKET MEDICAL DICTIONARY. *Giving the Pronunciation and Definition of the Principal Words Used in Medicine and the Collateral Sciences Including Very Complete Tables of the Arteries, Muscles, Nerves, Bacteria, Bacilli, Micrococci, Spirilla, and Thermometric Scales, and a Revised Dose-list of Drugs and Their Incompatibilities, in the English and Metric Systems of Weights and Measures, Based upon the Tenth Revision U. S. Pharmacopoeia; also a Revised Veterinary Dose Table.*
*By George M. Gould.*
*P. Blakiston's Son and Co.*
$2.00 $3\frac{1}{2}$ x $6\frac{1}{8}$ *Philadelphia*

A new edition of this standard dictionary, incorporating a selection of recent accessions to medical terminology. This pocket edition contains 40,000 words, is durably bound and handy as a ready reference where a comprehensive and detailed definition is not essential.

## EDITORIAL NOTE

The time seems to have come when it is desirable to make a formal and authoritative statement regarding the *New Biological Books* Section of THE QUARTERLY REVIEW OF BIOLOGY. This section appears to have met with rather widespread approval from the biological reading public since its inception, so far as the Editors have been able to judge from correspondence and conversation with scientific colleagues, and from the frequently so earmarked growth of the subscription list. This leads the Editors to suppose that the general editorial policy of this section has, on the whole, been favorably regarded by biologists generally. An occasional sour note has been heard from an author who thinks he has been unfairly treated in the notice of his book, but every such letter in our files is matched by at least one letter (and often more) from an equally distinguished biologist expressing hearty approval of the particular review in question.

One important element in the editorial policy relative to the book reviewing section of THE QUARTERLY REVIEW OF BIOLOGY has been that all reviews shall be anonymous. This anonymity has been preserved, and will be, with the utmost fidelity.

It has increasingly been made apparent to us, however, that there prevails a widespread notion that the Editor writes all, or substantially all, of the book notices appearing in this REVIEW. The chief purpose of this note is to correct this misapprehension. The Editor of THE QUARTERLY REVIEW OF BIOLOGY writes only a small fraction of the book notices which appear in its pages. The book reviews not infrequently express judgments and opinions entirely contrary to those of the Editor regarding the books concerned.

The Editors wish further to take this opportunity to state categorically that they assume no responsibility for opinions expressed or conclusions reached by authors of signed articles printed in THE QUARTERLY REVIEW OF BIOLOGY. Articles are accepted for publication because the Editors regard them as likely to be of interest, or of use, or both, to the biological public, and for no other reason. This is the total extent of the editorial responsibility. Outside of these limitations any writer in THE QUARTERLY REVIEW OF BIOLOGY is at liberty to say anything he likes. The responsibility for his utterances is his, not ours. We sometimes try to help him put his views in a form consonant with the literary and artistic standards which we try to maintain in the REVIEW, but *scientifically* he digs his own grave and erects his own monument.

R. P.